THE FEEDING ECOLOGY, PRODUCTIVITY AND MANAGEMENT OF STARLINGS IN CANTERBURY, NEW ZEALAND.

A thesis presented for the degree of Doctor of Philosophy in Zoology in the University of Canterbury, Christchurch, New Zealand.

by

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CHAPTER 1

INTRODUCTION

The starling Sturnus v. vulgaris L. is native to Western Europe, but through liberation now occurs widely throughout North America, South Africa, Australia and New Zealand. The species became established in New Zealand following nation-wide liberations between 1862 and 1883 (Thompson, 1922), and by 1895 occurred in immense flocks in nearly all districts (Kirk, 1895). In Canterbury, birds were liberated by Acclimatisation Societies in 1867 (20) and in 1871 (40) (Thompson, op. cit.). At approximately the same time, many birds were released by private citizens and starling numbers increased rapidly. Since that time the natural aggressiveness, adaptability and capacity for rapid colonization inherent in the species have led to its present widespread distribution in lowland Canterbury.

Apparently, starlings captured in Britain formed the bulk of birds liberated in New Zealand. However, birds from this source have been considered to show "marked differences in the degrees of development of their reproductive systems", and the existence of two local races has been postulated (Bullough, 1942) viz. a resident early-breeding British bird and a later breeding migrant European form. Amadon (1962) disagreed with this thesis and considered the Continental and British birds to be identical, and referred them to Sturnus v. vulgaris L. Although both "races" may have been included in the stock introduced into New Zealand, the Canterbury population appears to be phenotypically uniform.

Starlings are ubiquitous on farmlands of many countries and, because of their varied diet, have been frequently studied. Starling foods, feeding habits and breeding biology have been examined in detail in North America (Kalmbach and Gabrielson, 1921; Lindsey, 1939; Kessel, 1957; Howard, 1959), Australia (Thomas, 1957 a-e), Great Britain (Collinge, 1924-27; Dunnet, 1955, 1956) and Europe (Kluijver, 1933; Szijj, 1956; Shlapak, 1961; Karpovich, 1962; Pfabe and Szypula-Gador, 1964; Havlin and Folk, 1965; Gromadski, 1969).

There has been little work done on this species in New Zealand above anecdotal levels, but several research programmes are currently in progress e.g. Ecology Division, Department of Scientific and Industrial Research (D.S.I.R.), is studying the breeding biology and inheritance of clutch size in the Wellington area and its feeding and breeding biology at Havelock North. Published research includes a cursory study of starling foods and feeding on the Wellington and Gisborne airfields (Caithness, 1968), damage to fruit in New Zealand orchards (Dawson and Bull, 1970), and a list of the food species identified from the faeces of a group of Mid-Canterbury starlings (Lobb and Wood, 1971). The manipulation of starling populations in conjunction with stock as agents in biological control programmes has also been documented (Anon, 1970). Unpublished theses include the foods and daily movements of starlings on Harewood Airport, Christchurch (Moeed, 1970) and, predation on populations of Costelytra zealandica, a scarabaeid beetle (East, 1972).

Starlings may be beneficial or detrimental to agriculture depending on whether any increase or reduction in farm production results from their activities. In the mixed farming areas of Canterbury the feeding activities of the starling are diverse; the province includes the main cereal growing region of New Zealand and has extensive grasslands which frequently have high density populations of Costelytra zealandica White. This common food item of the starling (Anon, op. cit.; Lobb and Wood, op. cit.) is a serious economic pest, as it causes extensive damage to pasture grasses. Many farmers believe that starlings may partly control this invertebrate, and this has also been suggested by Dr R. East, an entomologist (cited by Bloxham, 1968). Recent laws controlling the use of once liberally applied insecticides have stimulated some farmers in Canterbury and elsewhere to erect nest-boxes throughout their farms, in attempts to entice and hold starlings on their properties. However, while the starling is the commonest bird species on most farmlands of New Zealand, much of its feeding ecology in this country is poorly documented. Studies of its food in other countries have shown that the species takes a wide range of pastoral invertebrates, but also severely reduces stocks of grain and fruit. It is therefore of great importance that all aspects of the local ecology of the

starling should be fully documented, before the species is considered for manipulated biological or integrated control programmes.

The aims of this study were, in order of priority:

1. to assess the foods and feeding biology of a population of starlings in a mixed-crop-livestock farming area of Canterbury,
2. to evaluate the species productivity and demography, and
3. to investigate the feasibility of manipulating local starling populations, with the view of capitalizing on their expected selected predation of certain invertebrates harmful to local agriculture.

Simultaneously, an associate study was made at Lincoln College, New Zealand, by Dr R. East (for details, see above); both studies have been instigated and partly financed by the New Zealand Department of Scientific and Industrial Research.

The first part of this thesis deals with methods of sexing and ageing starlings and population statistics. Subsequent sections, in order, deal with starling population management, demography, breeding biology, foods and feeding biology and changes in body weight.

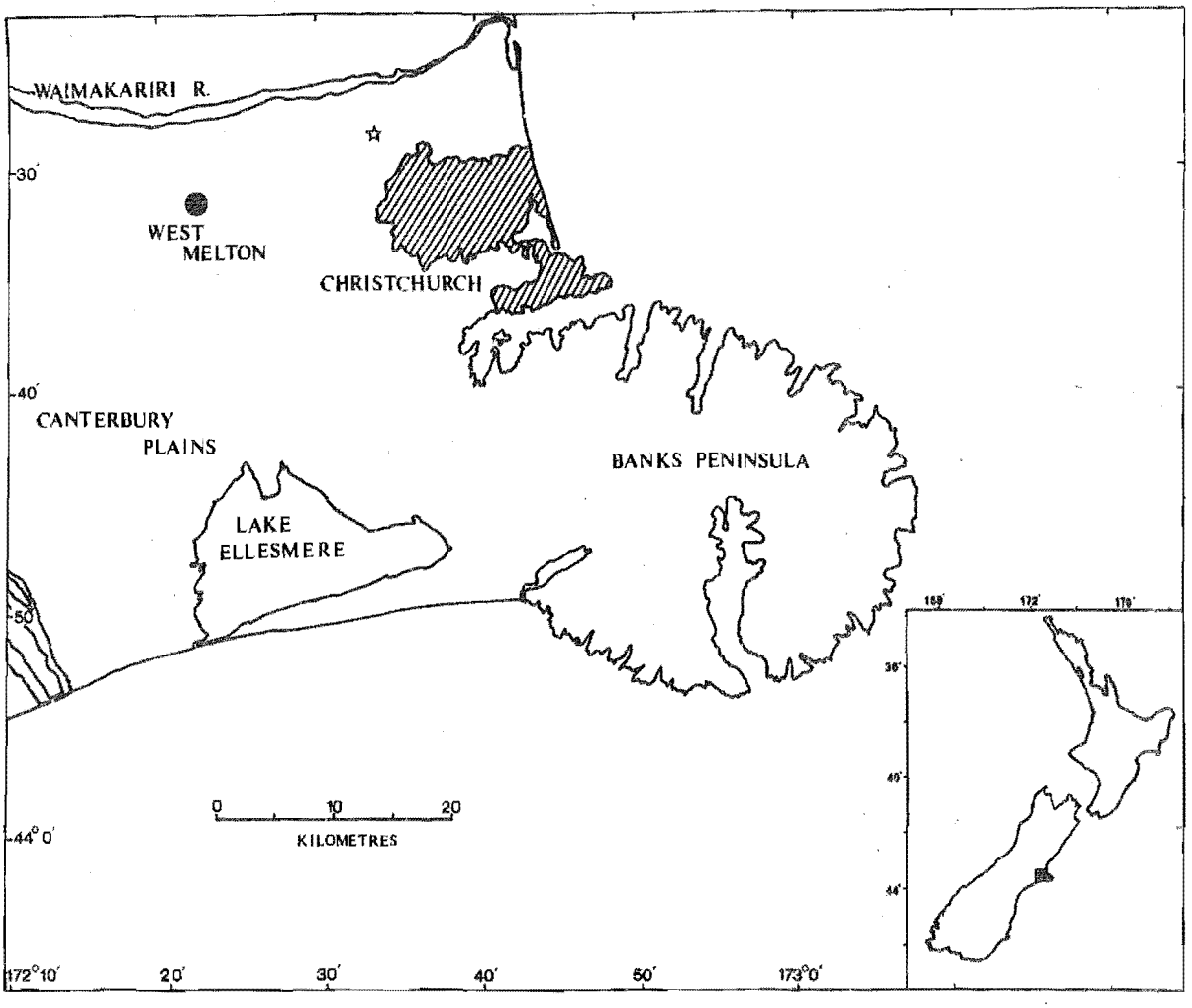

WAIMAKARIRI R.
30'
WEST
MELTON
CHRISTCHURCH
40'
CANTERBURY
PLAINS
BANKS PENINSULA
LAKE
ELLESMERE
50'
0
10
20
KILOMETRES
44° 0'
172° 10'
20'
30'
40'
50'
173° 0'

Fig. 1

Mid-Canterbury, showing the location of the study area - West Melton. Rainfall and temperature data were recorded at Harewood meteorological station shown thus - ☆ .

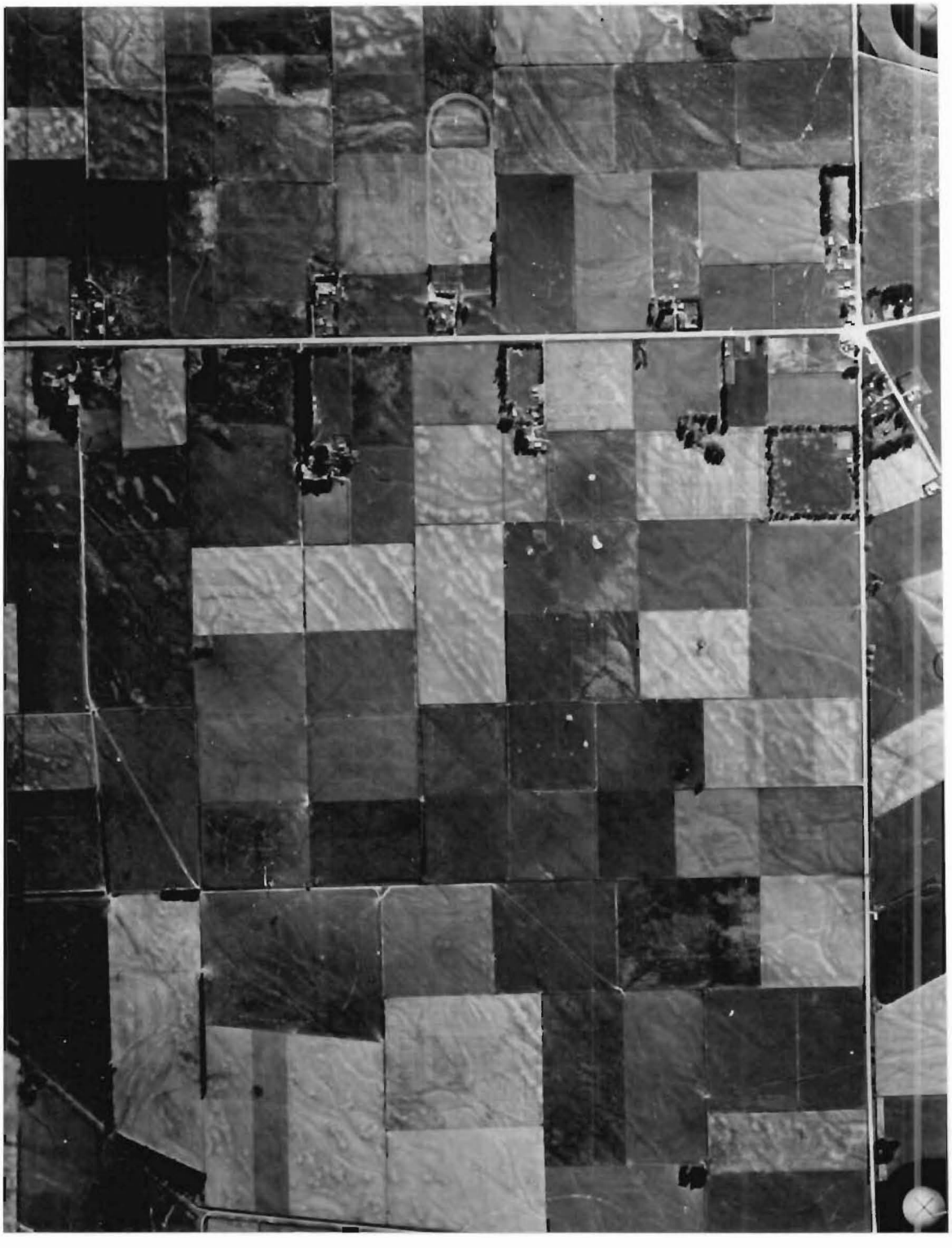


Plate 1

An aerial view of a representative part of the study area at West Melton (Crown copyright). Note the clumping of farm buildings and of trees.

CHAPTER 2

STUDY AREA

The study area at West Melton covers approximately 75 km^2 on the North Canterbury Plains (Fig. 1). This extensive area of flat land is characterized by yellow-grey earths in association with gravelly or stoney soils, whereas recent alluvial soils occur near the coast and extend up the larger river beds (McLintock, 1960: Figs. 11 & 13). Within the study area, Hatfield sandy loams occur in the south and west, and Paparoa sandy loams in the north and east; both soils are free draining, moderately fertile and suitable for extensive cropping. The rainfall is low (58-78 cm annually at Harewood, 14 km away), and summers are warm with occasional hot north west Foehn winds of above 30^{o} C; the winters are cool with frequent frosts and occasional light snow (Fig. 2).

Farming consists largely of the production of livestock (sheep and cattle, see Appendix I for generic and specific names) and mixed cash crops viz. wheat, barley, oats and potatoes, with occasional stock fodder crops viz. turnips, rape and choumoellier. Indigenous vegetation (largely tussocks) has been replaced by lucerne and exotic grasses, while gorse and exotic tree species occur frequently as shelter belts (Plate 1).

Starlings at West Melton live alongside a wide range of feral mammals and birds. Cats, stoats and hedgehogs frequent shelter belts, whereas hares and rabbits occur in open fields. Common birds include rooks, white-backed magpies, gulls, house sparrows and rock pigeons.

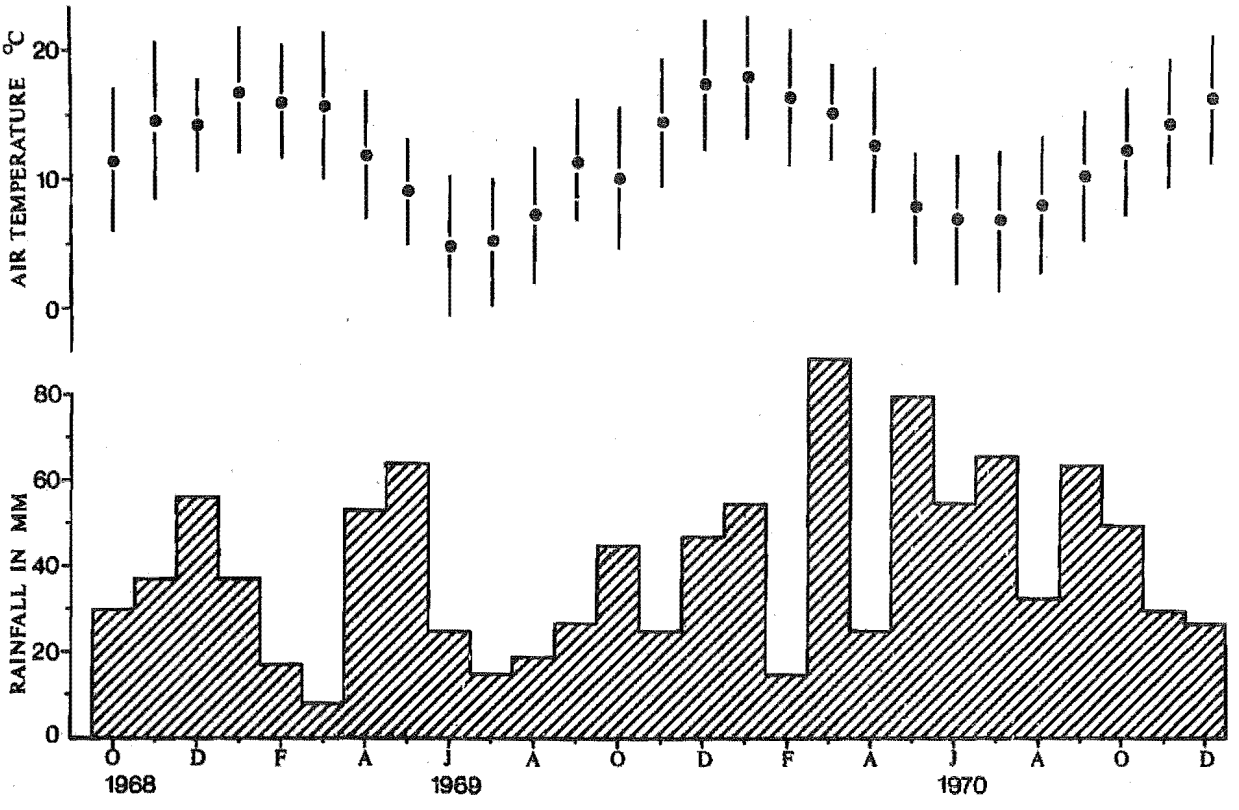

AIR TEMPERATURE °C
20
10
0
RAINFALL IN MM
80
60
40
20
0
O
D
F
A
J
A
O
D
F
A
J
A
O
D
1968
1969
1970

Fig. 2

Rainfall and temperature recorded during the study at Harewood meteorological station (see Gabites, 1968, 1969, 1970). Temperature data are represented by a monthly mean (●) and the mean daily maximum and minimum temperatures for the month (the vertical bar).

CHAPTER 3

THE DETERMINATION OF SEX AND AGE

1. INTRODUCTION.

It is important in ecological studies of vertebrates to be able to accurately determine the age and sex of the study animal. Both determinations are problematical for many bird species, and the starling is no exception. Sex has been determined most accurately for this species by Parks (1962) and Schwab and Marsh (1967), who used a combination of the iris and mandibular rami colours; the latter authors being correct for 97.6% and 97.7% of males and females respectively. Age has been determined by Bullough (1942), Kessel (1951), and Davis (1959) from the length of the iridescent portion on the lower throat hackles of birds in adult plumage, two age classes being recognizable; birds of less than 12 months old, and those older. Both methods were used and critically examined by the author for their accuracy for starlings in Canterbury.

Approximately 40 birds were shot each month between 1000 and 1500 hr during the period April 1969 to March 1970. Carcasses were examined on the day of collection as the colour of some organs faded rapidly with refrigeration. Additional information was gathered from breeding birds taken live at nest sites.

Each carcass was cursorily checked for the colour of its irides, mandibular rami and general plumage, and later the extent of its throat hackle feather iridescence. Predictions of both age and sex were checked using birds of known age and by autoptic studies of gonads and the bursa Fabricii; the latter a bulbous lymphoid sac opening into the upper cloaca. For hackle iridescence, four of the longest most attenuate hackles present on the birds forethroat were plucked from each starling, and the iridescent portion of each (minus the white tip) measured to the nearest millimetre, using a stereoscopic microscope fitted with a graduated eyepiece. Iridescence means calculated for each bird were analysed by the use of

Harding's (1949) method of polymodal frequency distribution analysis as revised by Cassie (1950), and linear transformations were obtained of the component groups of the size frequency distributions present. Such analyses permitted a ready detection of overlapping data of such groups, the point of inflexion in each bimodal frequency distribution corresponding to the low points of a frequency diagram.

2. RESULTS

I. Determination of sex

Eye colour in adult starlings was dimorphic (Table 1). In females the iris was edged by a broad band which ranged in colour from light lemon to deep orange, and enabled ready identification in 96% of all females examined. Most males (67.3%), however, possessed a uniform deep-liver-coloured iris. The remaining birds of both sexes possessed irides peripherally marked by a narrow faint yellow band, and determination of sex was difficult. All birds attained adult eye colour characteristics by the end of their first moult (Table 2) and retained them thereafter.

Table 1. THE RELIABILITY OF SECONDARY SEX CHARACTERISTICS IN BIRDS OF ADULT PLUMAGE.

	Males		Females	
	No. examined	Percent composition	No. examined	Percent composition
Iris colour				
Identification positive	76	67.3	72	96.0
Character indecisive	37	32.7	3	4.0
Bill ramus colour				
Identification positive	113	100.0	73	97.3
Character indecisive	Nil	Nil	2	2.7
Both characters combined				
* Identification positive	113	100.0	74	98.7

Note - * Ignores single indistinct character of any pair

Bill colour was also dimorphic (Table 1) but varied seasonally. Birds of either sex had uniformly dark bills in mid and late summer (January - March), which changed to a bright lemon yellow in early winter (April - May) over a period of four to six weeks (Table 2). Concurrently, the rami of the lower mandible turned blue to blue-black in all males examined and light pink in 97% of all females; the remaining females had bills which were entirely lemon-yellow. A subsequent reversal in colour began distally and occurred prior to and during the post-nuptial moult.

Table 2. SEASONAL VARIATION IN AGE AND SECONDARY SEX CHARACTERISTICS

Age/Sex character	Month of Collection											
	J	F	M	A	M	J	J	A	S	O	N	D
Juvenile Plumage present	1	15	7	-	-	-	-	-	-	-	-	12
Bursa Fabricii present	1	15	6	-	-	-	-	-	-	-	-	12
Adult bill colour												
(a) Wholly black	17	15	18	35	10	1	-	-	-	-	-	2
(b) Intermediate but without secondary sex character	-	-	-	12	9	6	-	-	-	-	-	5
(c) Wholly yellow with secondary sex character present	-	-	-	-	4	41	35	39	36	37	12	16
N	18	30	25	47	23	48	35	39	36	37	12	35

II. Determination of age

Young starlings retained a dull grey-brown plumage for approximately 12 weeks following fledging (Table 2) and had grey eyes and grey-black bills, the latter at first edged with bright yellow wattles. They moulted between January and the end of March, and attained a typical dark spangled adult plumage indistinguishable from that of older birds. Autoptic studies

revealed that the moult of the fledgling plumage occurred concomitantly with the regression of the bursa Fabricii (Table 2), as this bursa was discernable in only two birds in full adult plumage.

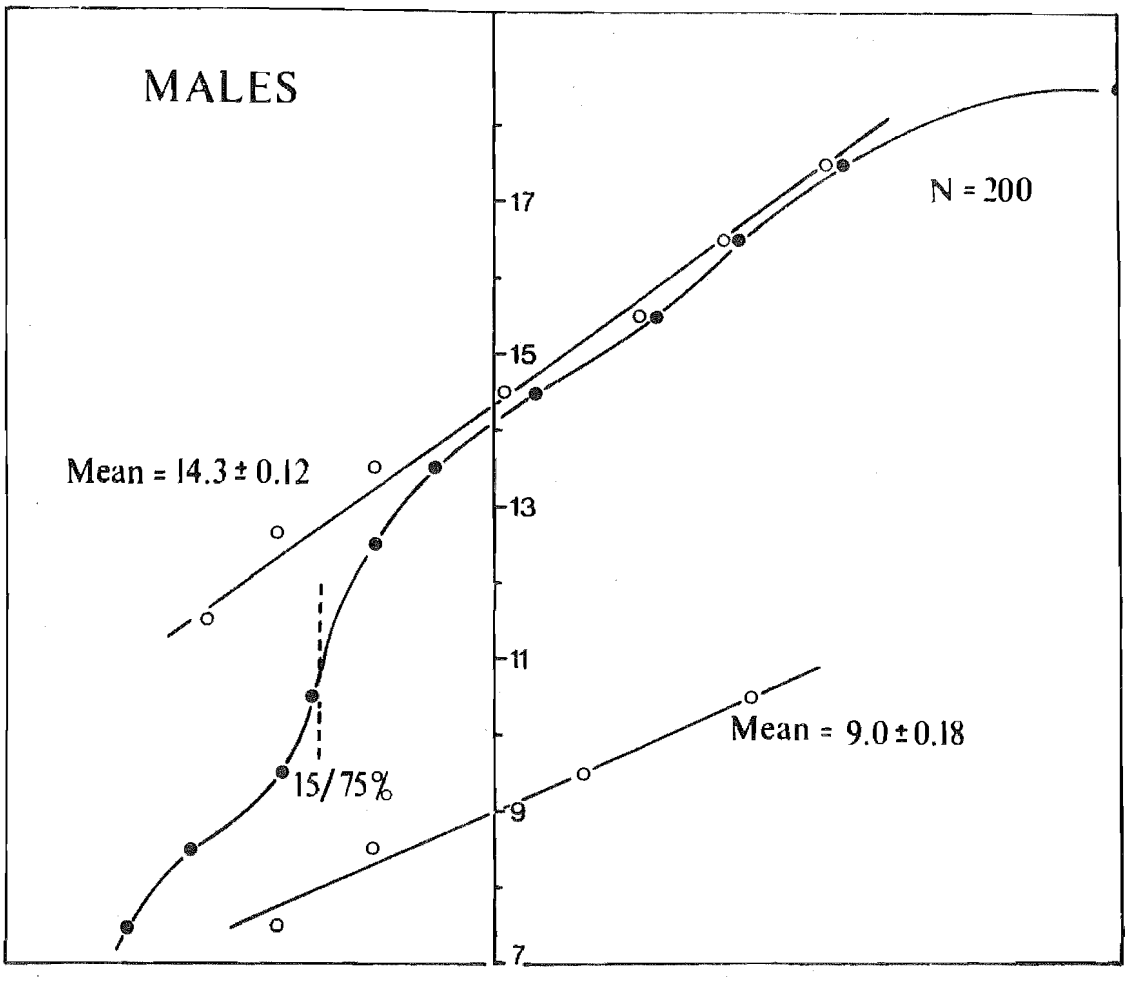
The length of the iridescent portion of hackle feathers in birds of either sex was bimodally distributed (Fig. 3); the two component groups within each sex representing (1) birds of less than 12 months of age and (2) those older. Males and females respectively had mean iridescence values of 9.0 $\pm$ 0.18 and 5.6 $\pm$ 0.05 mm in the shorter hackle group, and 14.3 $\pm$ 0.12 and 9.5 $\pm$ 0.13 mm in the longer hackle group. Numbers in the first group were low, due largely to young birds in adult plumage being present in the population for little more than half of their first year.

The overlapping flanks of the frequency distributions of each component group within each sex were separated out (Table 3), thus dividing each sex into three possible classes. Starlings with iridescence values of 6 - 7 mm in females and 10 - 12 mm in males were considered of indefinite age (Group B, see Table 3) and the remainder of each component group fell into either group A or group C (Table 3). Proportionately more females than males fell into the indefinite category, as the two component groups of females were compacted into a smaller range.

Table 3. THE COMPONENT GROUPS WITHIN THE SIZE FREQUENCY DISTRIBUTIONS OF HACKLE FEATHER IRIDESCENCE.

Size Class	Females			Males		
	N	Percent Occurrence	Group Limits (mm)	N	Percent Occurrence	Group Limits (mm)
Group A	8	5.4	<6	22	11.0	<10
Group B	22	14.9	6-7	26	12.9	10-12
Group C	118	79.7	>7	153	76.1	>12

Groups A and B of both sexes included a few individuals


MALES
N = 200
Mean = 14.3 ± 0.12
15/75%
Mean = 9.0 ± 0.18
17
15
13
11
9
7

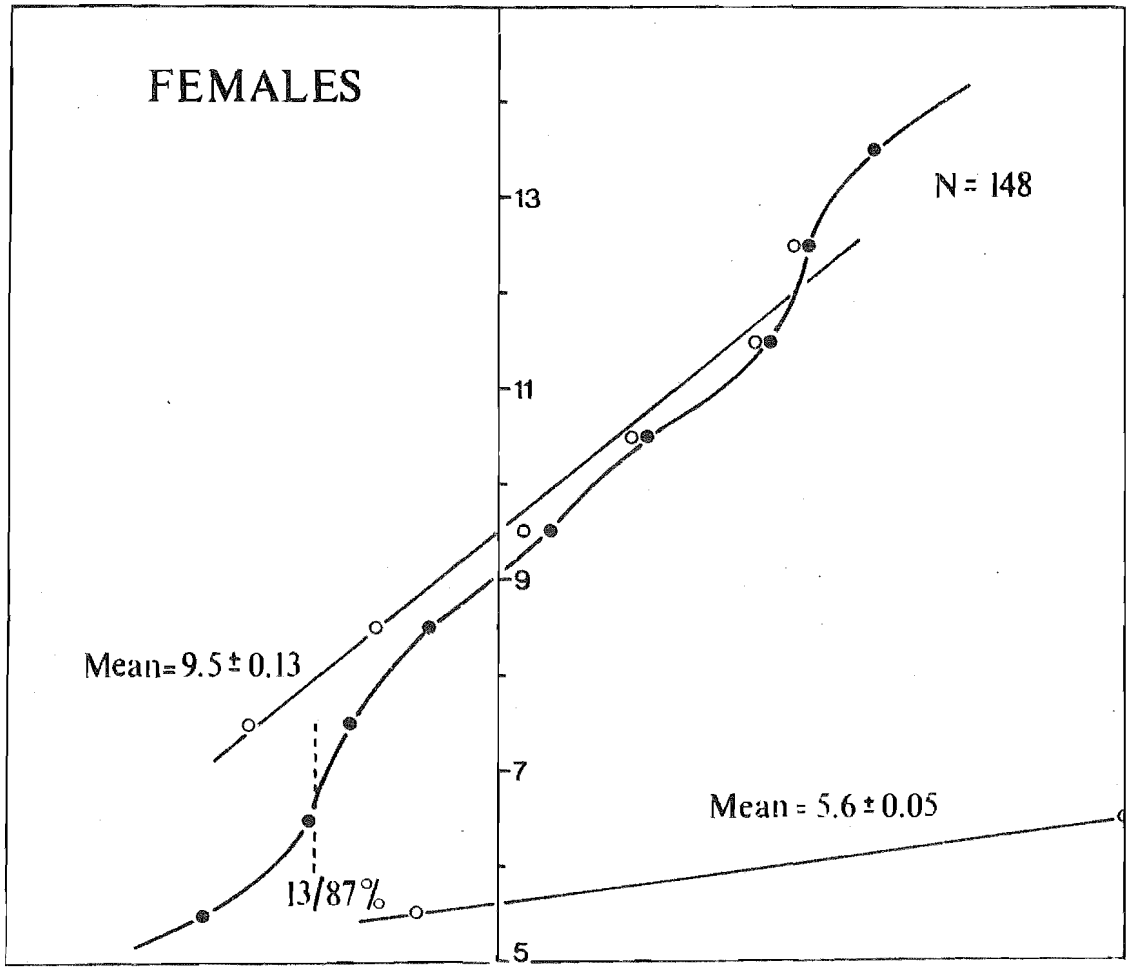

FEMALES
N = 148
Mean= 9.5 ± 0.13
13/87%
Mean = 5.6 ± 0.05
13
11
9
7
5

Fig. 3

The determination of the parameters of overlapping normally distributed component groups, indicated by hackle feather measurements (the Y coordinate). The second inflexion in the curve plotted for females has been ignored, as it concerns less than 5% of birds measured.

of less than 12 months old, with adult or partially adult plumage and a distinct bursa Fabricii. Conversely, the hackle iridescence of 92 adults recaptured while breeding for the second year, and therefore at least two years old, all fell into group C. Likewise, two birds banded as nestlings and trapped two years later had hackles within the group C range.

3. SUMMARY

Starlings can be sexed by the sexually dimorphic iris and mandibular rami colours. Iris colour is a less reliable criterion, especially for males (67% accuracy), than the colour of the bill rami (2.7% error), but the latter can be used only from May to December. By using a combination, and ignoring single indistinct characters, the criteria distinguish males without error and females almost so (98.7%).

Following the moult of a distinctive juvenile plumage, all starlings are superficially alike. However, the length of the iridescent portion of the lower throat hackles varies with age. Length frequency distributions of hackle iridescence show two groups within either sex representing birds in their first year, and those older. Using this criterion, the ages of a small proportion of starlings (13% of males, 15% of females) cannot be determined, but all birds of known age fall into the correct group. Iridescence values show a partial separation with sex, but measurements for first year males and older females overlap, thus the character is unreliable for sex determination.

CHAPTER 4

POPULATION STATISTICS

1. INTRODUCTION AND METHODS

The annual mortality of most birds is high in their first year but lower and approximately constant thereafter (Farner, 1945; Kendeigh, 1961). Starlings are no exception; most overseas mortality estimates are similar but show distinct age variations e.g. 66 and 53% for first year and adult birds respectively in Belgium (Delvingt, 1962), 66 and 55% in Britain (Lack, 1948), 73 and 62% in Switzerland (Lack, op. cit.) and 60 and 50% in North America (Kessel, 1957).

Mortality rates are apparently sex specific; sex ratios at fertilization are perforce approximately 1:1, yet with one notable exception (see Loefer and Patten, 1941), in winter starling populations contain an excess of males e.g. estimates of live male free-flying birds vary from 71.1% (Bullough, 1942) to 75% (Coulson, 1960) in Europe, and from 52.2% (Stegeman, 1954) through 56.6% (Thompson and Coutlee, 1964), 57.2% (Davis, 1959), 57.3% (Kessel, 1957) to 68.3% (Hicks, 1934) in North America. Disproportionate ratios have been recorded amongst nestlings e.g. approximately 60% females (Kessel, op.cit.), but more balanced ratios amongst first year birds e.g. 52% males, Davis, op.cit; 51% males, Kessel, op.cit. Although dimorphic adult roosting patterns could account for some of the disparity, its universality points to differential mortality of females.

Knowledge of population structure is basic to any general ecological study and especially so in the present, where efforts were made to increase local starling populations. The present section covers population size, longevity, mortality and sex ratios and, following a posteriori discoveries, attempts to explain the preponderance of males.

Population estimates were made at roosting, feeding and breeding sites (for methods at breeding sites, see Ch. 5.2.I). Starlings were counted at roosts either as they arrived or left normally, or after being startled into the air by noise; at

feeding sites they were counted during weekly farm censuses. (See Ch. 6.2).

Adult mortality was estimated from capture-recapture studies of occupants of four artificial "colonies" (44 boxes) during 1969, 1970 and 1971. Mortality of younger birds was estimated from recaptures of breeding birds banded as nestlings. The sex of 406 free-flying birds was determined by autopsy following their collection at feeding sites during 1969 and 1970. Carcasses were aged by hackle-feather determinations and separated into first year and older birds. Nestling sex ratios were determined by the autopsy of 84 birds taken from natural sites in 1971.

Sex ratios of all birds were tested by Chi-square analyses for goodness of fit to a 1:1 ratio and Yates correction factor for small samples incorporated.

2. RESULTS

I. Population estimates

In mid-winter, 1969, starlings occupied six communal roosts within or peripheral to the area covered by the census route (Fig. 4). Bird numbers were lowest during breeding (roosts often being deserted then), when females roosted in nests and males occupied small communal roosts nearby, and highest in mid-winter (June and July) e.g. successive counts at roosts 1 and 4 (Fig. 4) were respectively - Feb. 10 - 20, 40; March 3 - 109, 46; May 5 - 200, 61; June 7 -187, 49; July 14 - 400, 87; Aug.1 - 0, 81. Peak winter roosting numbers at local roosts ranged from 50 to 400 and totalled 1150. Although small (<100) mid-winter roosts may have been missed, the error involved is thought to be small.

The monthly density of birds in the area censused ranged from 0.159 to 0.551 / ha throughout the year, and averaged 0.334 ± 0.0338 birds / ha (c.f. maximal densities of natural breeding populations of 0.14 birds / ha; see Ch. 5.3.I). As the area enclosed by the census route was 18.5 km^2, the number of starlings feeding within it was 618 ± 63; a conservative estimate as some birds may have been resting in nearby trees during each census. Feeding numbers were lower than those obtained at roosts, but some roosts were peripheral and

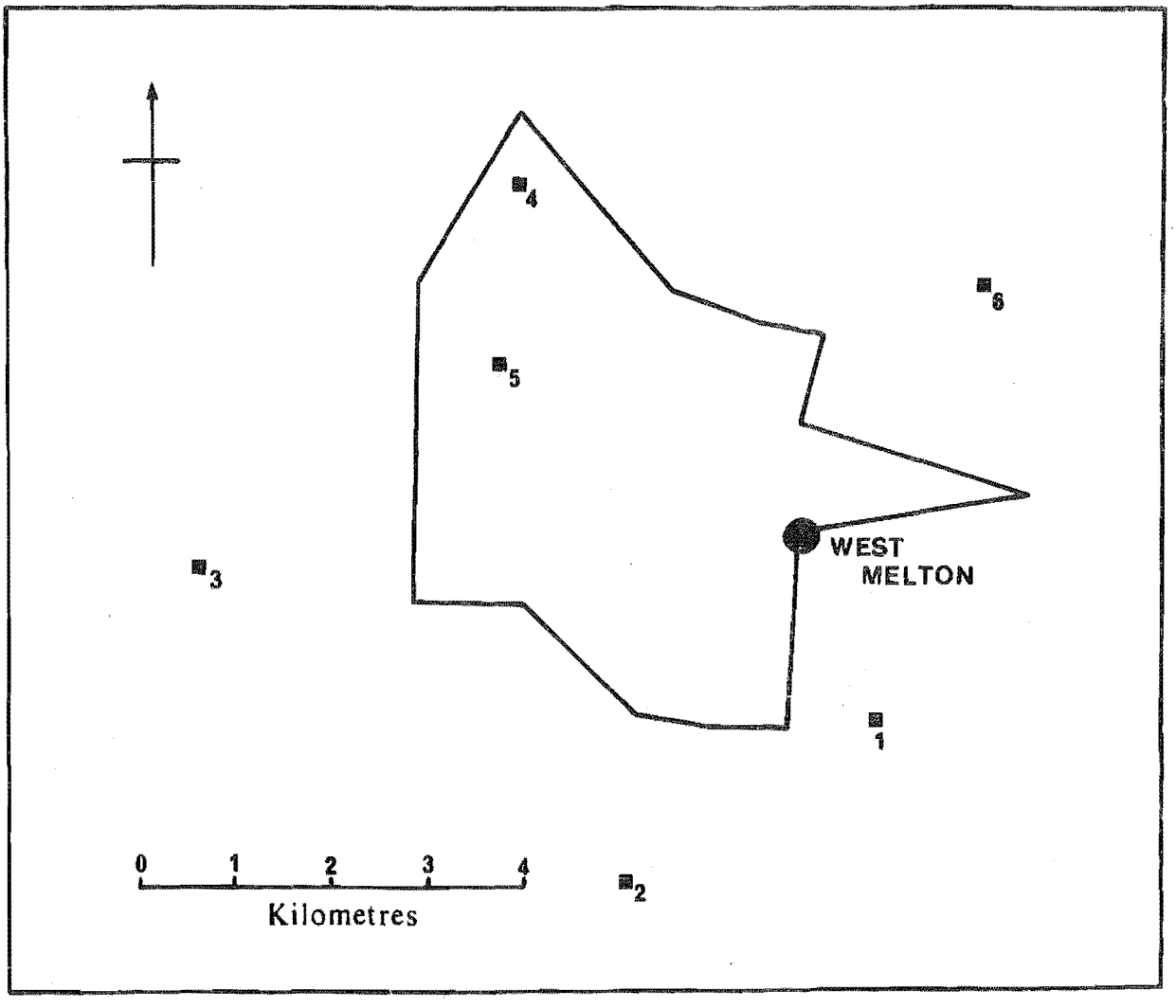

4
6
5
WEST
MELTON
3
1
0
1
2
3
4
Kilometres
2

Fig. 4

The location of communal roosting sites of starlings in mid-winter about West Melton. The census route is also shown.

undoubtedly attracted birds from neighbouring areas.

II. Mortality and longevity

The rate of box occupation and capture of female occupants varied each year e.g. 30 females captured from 34 occupied sites in 1969, 40 females from 44 sites in 1970 and 30 females from 32 sites in 1971. Fifteen females were recaptured in 1970, and eight of these captured for a third time in 1971. With one exception (2%), females bred in the same colony each year, and annual mortality, determined directly from the recaptured samples, was 50 and 53% in 1970 and 1971 respectively (a minimal estimate as a few occupants were not captured in these years). Adult males were captured less frequently and data from them were sparse.

First year mortality was determined indirectly; those alive after two years being estimated at 11.8% (see Ch. 5.3.III) c.f. 17% for similar-aged birds in Holland (Kluijver, 1933), and 20% in North America (Kessel, 1957). As I have little information on the dispersion of young birds, survivorship in this age class may be considerably higher.

Longevity records are few and concern females only. During the entire study, 11 females were captured breeding for their third successive season and thus were three and probably four years old. Some birds in the population are probably older than this, as the potential longevity of any species is considerably greater than that commonly recorded in the field (Bourliere, 1946). Elsewhere in New Zealand, a starling in its ninth year has been recorded (Robertson, 1972) and in Europe birds aged 12 and 16 years recovered (Lack, 1948; Jirsik, 1934 respectively).

III. Sex ratios

The male:female ratio of Canterbury nestlings (1.27:1) did not differ significantly from 1:1, and neither did it for the 73 first-year birds examined (1.28:1). Males were collected more frequently throughout the year but the size of the seasonal samples limited analysis.

In adults, males were again preponderant throughout much of the year, being significantly so in winter and in yearly totals (Table 4).

Table 4. SEX RATIO OF 270 ADULTS STARLINGS COLLECTED AT WEST MELTON.

	Season of Collection				
	JFM	AMJ	JAS	OND	Annual
No. of males	28	58	49	23	158
No. of females	19	34	36	23	112
X^2 adjusted value	1.362	5.750	1.714	-	7.500
Level of significance*	n.s.	*	n.s.	-	**

Note: * for explanation of level of significance, see Ch.5.2.III.

Adults of either sex were collected with equal frequency in spring, but this reflects the collecting technique rather than existing ratios; spring samples were collected alongside natural breeding sites and frequently contained mated pairs.

3. DISCUSSION

Approximately 1150 starlings roosted in mid-winter communal West Melton roosts, but fewer were present at other times of the year (similar trends were shown by starlings in Britain; Symonds, 1965). The numbers roosting were larger than the estimated feeding or breeding populations within the study area; the additional birds were from neighbouring areas.

Mortality and longevity estimates of adult females agree closely with overseas findings. Considerably higher mortality than that of adults occurs amongst local sub-adults, but this estimate may have been affected by post-fledging dispersion. Lack (1946), Coulson (1960) and Kessel (1957) considered that the bulk of first year mortality occurred during summer and autumn but in the present study this remains unproven.

Like overseas populations, the sex ratio of adult Canterbury birds is significantly weighted towards males. Sex ratios of most birds are close to 1:1 at hatching (Mayr, 1939; Lack, 1954, p 10) but as ratios of local nestling and first year starlings are balanced, some differential mortality factor must be operating against females aged 12 months or older c.f. Mayr (op.cit) who considered that dimorphic mortality occurs at all life stages in most animals. Unbalanced ratios apparently arise from dimorphic adult behaviour during the breeding season;

dimorphic behaviour in other seasons is minimal and males and females feed, flock and roost together. Females carry out a disproportionate amount of the incubation and feeding of nestlings (see Ch. 6.3.I) and are differentially vulnerable to predators at this time, several being taken from nests by stoats. Davis (1959) and Coulson (1960) similarly considered that differential mortality of the sexes following the first 10 months of independent life resulted from the females' breeding activities, especially as some females but no males breed in their first year. Further, physiological stresses associated with laying and purported to lead to differentical mortality in the tree duck Dendrocygna autumnalis (Bolen, 1970) may do likewise in starlings; first year females have less food reserves than first year males or older birds (see Ch. 8.2.III) and those that breed are probably ill-equipped to do so.

CHAPTER 5

BREEDING BIOLOGY

1. INTRODUCTION

Knowledge of the breeding biology of the starling is essential for complete understanding of the species feeding ecology, for it is when the nestlings are present that starlings prey most heavily on selected invertebrates. It was thus necessary to estimate starling productivity and to determine the diet of the young (for nestling foods, see Ch. 6.3.V). In addition, as many of the prey are harmful to local agriculture, nest boxes were erected in an effort to increase starling densities locally so as to capitalize on their predation of harmful invertebrates found in farm lands.

Overseas, comprehensive studies of the breeding biology of starlings have been made by Kluijver (1933), Dunnet (1955), Kessel (1957) and Collins and De Vos (1966), but this is the only detailed study so far in New Zealand. Data were collected from breeding birds at West Melton (for a description of the Study area, see Ch. 2) during three successive breeding seasons, 1968, 1969, and 1970, with additional information collected in 1971.

2. METHODS

I. Natural and artificial populations

The limits imposed on starling numbers in spring by food and nest site availability were examined by comparing the densities of starlings which bred in natural sites with those in artificially established colonies. Natural populations on a 345 ha farm were censused in 1969 and 1970 during early and late November, using methods described by Williamson and Homes (1964). Thus I located breeding sites by listening for starling vocalizations, by looking for nestling droppings and by following adults carrying food to nestlings. All nests were checked for the presence of eggs or chicks to eliminate those "occupied" by non-breeding birds.

Plate 2

The form and sites of nest boxes erected about West Melton. Boxes were frequently placed on exposed fences or amongst hedgerows.

(Photographs - H.A. Best)

Artificial breeding colonies of starlings were established by the erection of 101 nest boxes in the late winter of 1968, 105 (total 206) in 1969, and seven (total 213) in 1970 (Fig. 5). All boxes were constructed of "treated" Pinus 1.3 cm thick, and had inside dimensions of 20.0 x 15.2 x 15.2 cm. The roof member was hinged at the rear, but fastened in front for easy inspection, and the entrance was either a circular hole 5 cm in diameter, or a slot 5 cm deep adjacent to the roof (Plate 2). In 1968, all boxes were placed in hedgerows or on farm buildings at heights greater than 5 m, but in subsequent years many were lowered for easier observer access, and additional boxes placed either contiguously or on open fencelines; the latter were equipped with a support 50 cm long and covered with sheet tin to prevent entry by mammalian predators. Following the breeding season of 1968, isolated boxes were resited more centrally, and those damaged by stock replaced.

II. Age and breeding statistics

To determine the breeding phenology and productivity of starlings twice weekly visits were made around mid-day to all occupied sites during the pre-egg, egg, and nestling periods. Simultaneously, adult starlings were trapped for age and demographic studies. At first they were taken manually from the nest, but later were trapped with a pole-net, as suggested by Dunnet (pers. comm.), as they fled from the box entrance. Additional birds were taken from boxes at night, and similar trapping efforts were made outside breeding seasons. All adults and nestlings captured were identified with serially numbered metal bands, and approximately half of the captured adults marked with standard "colour bands" for distant recognition. In all, 8 adults and 108 nestlings were banded at nest sites in 1968, 87 adults and 212 nestlings in 1969, 166 adults in 1970 and 35 adults in 1971. Many of the birds captured in 1969, 1970 and 1971 had been banded by the author previously.

The age and time at which starlings first bred were determined by capture-recapture studies and from the linear measurements of the gonads of birds aged by hackle feather measurements. Gonads were collected throughout the study, fixed in Bouins solution and cleared with methyl alcohol; subsequent shrinkage was assumed to be constant. Later, the longest testis

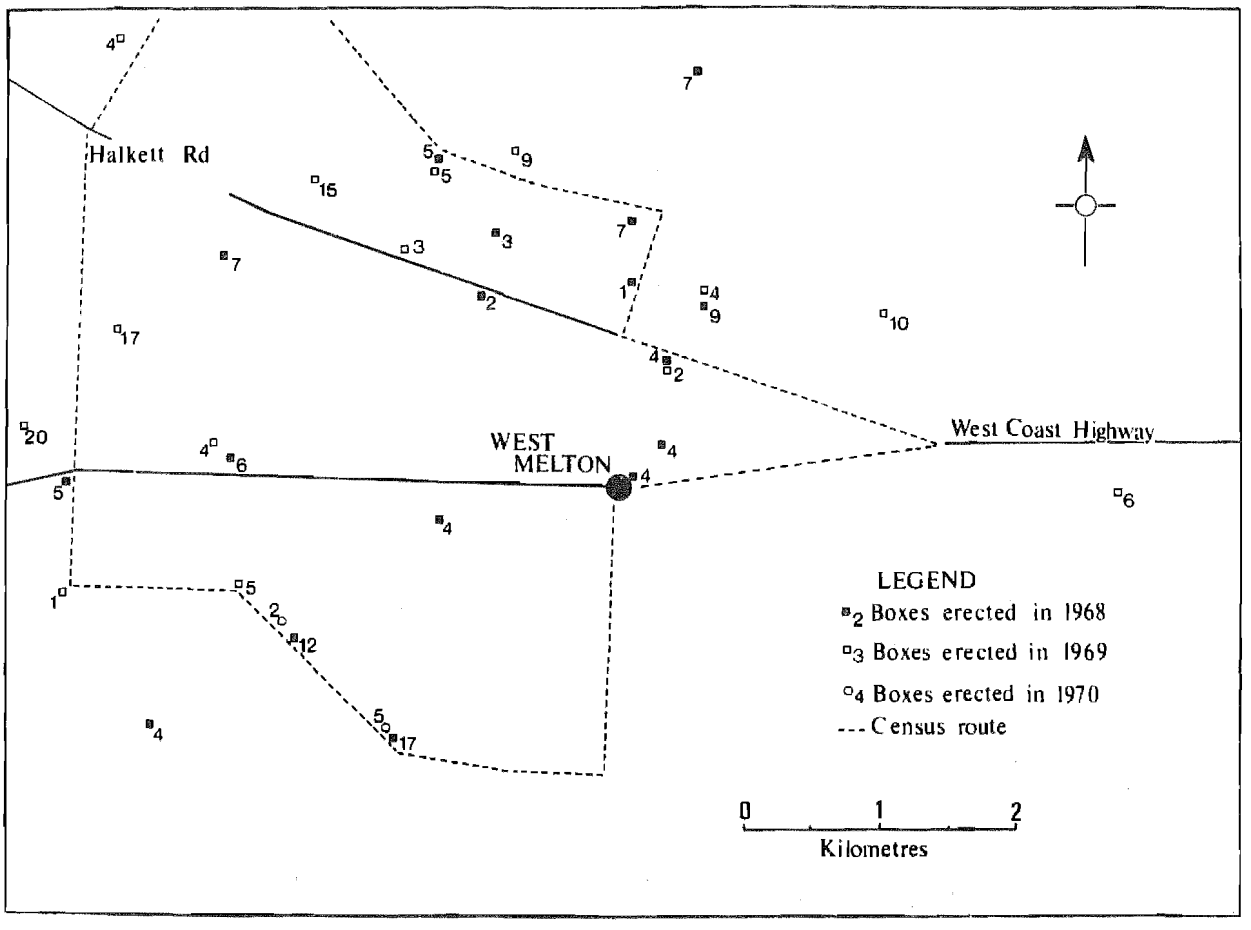

Halkett Rd
WEST MELTON
West Coast Highway
LEGEND
2 Boxes erected in 1968
3 Boxes erected in 1969
4 Boxes erected in 1970
--- Census route
0 1 2
Kilometres

Fig. 5

The location and numbers of nest boxes erected about West Melton during the study. A few boxes were destroyed by stock each year and isolated boxes re-erected more centrally for easier observer access.

present in each male (usually the left) and the diameter of the largest oocyte visible on the ventral surface of the ovary of each female, were measured to the nearest 0.01 mm, using a stereoscopic microscope fitted with a graduated eyepiece accurate to 0.01 mm. In young females, ovaries were cut open as the largest oocytes were often obscured by the overlying germinal epithelium.

III. Analysis of data

Statistical methods used in this thesis were generally taken from Sokal and Rohlf (1969). Computations were made on either a CANOLA-164 P electronic desk calculator or an IBM 360/44 computer. Programmes were selected for use from the Department of Zoology Standard Programme Library. Others were written by Mrs S.M. Robson.

All data were screened and tested for normality of distribution with Programme A-1 before applying more advanced parametric computational methods. A-1 lists the basic statistics of location and dispersion, compares the sample with the expected frequency distribution, and indicates any transformation code necessary to normalize non-normal data. Other programmes or statistical tests used have been listed in the text. The present chapter includes the student "t" and Kruskal-Wallis (H) tests for paired samples with homogeneous and heterogeneous variances respectively, and correlation analysis for estimating the association between variables. Breeding statistics were determined from programmes written by S.M. Robson.

Means and standard errors (S.E.) have been given for most samples. Statistical significance was determined at the 0.05% probability level and generally denoted by * where $0.05 > p > 0.01$, ** where $0.01 > p > 0.001$ and *** $p < 0.001$.

3. RESULTS

I. Natural breeding populations

The number of starlings which bred in "natural" sites over 345 ha, increased from 17 pairs (0.05 / ha) in 1969, to 23 pairs (0.07 / ha) in 1970 (Table 5). Most nests were in cavities in farm buildings, but a few were in fence posts, haystacks and hedgerows. Many were sited in loose colonial

Table 5. THE BREEDING DENSITIES OF STARLINGS ON 345 Ha OF FARMLAND AT WEST MELTON

Site of Nest	Date of Census			
	1969		1970	
	5.11.69	17.11.69	6.11.70	24.11.70
Farm buildings	12	13	15	16
Trees	3	3	5	6
Fenceposts	1	1	1	1
Total	16	17	21	23

units, similar to the nesting associations of most Carduelinae finches (Lack, 1968, p26), although isolated nests were also found. Colonies result from the clumped occurrence of available sites, and not from a preference for colonial nesting; most Sturninae being solitary nesters (Lack, op. cit. p142). Counts of birds about buildings may have been low, as observation was difficult, but probably all starlings breeding in the vigorous hedgerows were counted. Nest boxes were erected on the periphery of this farm in 1968, and were present in 1969 and 1970. However, as the numbers of starlings in natural sites nearby increased in this period, the birds which occupied the boxes could not have been attracted from nearby natural sites.

Table 6. THE RATES OF OCCUPATION OF NEST BOXES BY STARLINGS

Year	Boxes present	Box Utilization		
		Laid in	Nest built	Unused
1968	97	67 (69.1)	6 (6.2)	24 (24.7)
1969	198	143 (72.1)	39 (19.7)	16 (8.2)
1970	195	160 (82.0)	16 (8.2)	19 (9.8)

II. Artificial breeding populations

The occupation of boxes by starlings increased absolutely each year, and rose from 67 pairs in 1968 to 160 pairs in 1970 (Table 6). Birds bred in the same or in adjacent sites in

successive years (see below), and the increases reflected real changes in total local breeding populations.

Table 7. THE OCCUPATIONAL HISTORY OF INDIVIDUAL BOXES

Box status	N	Percent composition
Boxes occupied in all three years	57	76
Boxes never used	9	12
Boxes occupied in two years or less	9	12

Note: Only boxes present at the same site for the three years of study considered.

Individual boxes were generally either consistently used or avoided (Table 7); the status of 88% of all boxes remained unchanged after the first year. Thus, although there was strong annual competition for many sites, others were ignored throughout the study.

Table 8. NEST BOX OCCUPANCY IN 1968 IN RELATION TO THE SHAPE OF BOX ENTRANCE

Shape of Entrance	Number of Boxes Present	Number Occupied
Circular	43	41 (95.5)
Square	29	20 (67.8)

Note: For uniformity, only boxes in hedgerows were considered.

Starlings preferred boxes with circular entrance holes to those with larger slot-shaped entrances (Table 8). Nest bowls were constructed as far as possible from the box entrance, and boxes with excessively large openings were less satisfactory (also shown by McGilvrey and Uhler, 1971). Starlings preferred boxes sited in hedgerows to those on farm buildings or on fence-

lines (Table 9), because human disturbance was less (also shown by Verheyen, 1969a). As in Belgium (Verheyen, op.cit.), starlings selected boxes placed highest (Table 10); a result of the birds initially searching for nest sites in the tops of trees and buildings and working down (Plank, 1967).

Table 9. NEST BOX OCCUPANCY IN RELATION TO SITE

Site of Box	Number of boxes present	Number of boxes occupied	Percent occupancy
Hedgerows	72	61	84.9
Barns	25	6	24.0
Exposed fencelines	56	38	68.0

Table 10. TOTAL BOX OCCUPANCY IN 1969 IN RELATION TO NEST HEIGHT*

Height of box	Number of boxes present	Number Occupied
< 2m	18	16 (89.0%)
2 - 5m	10	10 (100%)
>5m	38	38 (100%)

* Considers only boxes with circular apertures erected in hedgerows.

Starlings appeared to lack any preference for cavity substrate when selecting nest sites (also recorded by Plank, op.cit.); artificial and natural nests being found in a wide range of sites and positions.

The number of starlings which bred in artificial "colonies" reached a maximum of 15 pairs, many of which bred successfully. As birds foraged up to 0.5 km away from the nest during breeding (see Ch. 6.3.I), densities of 0.19 pairs / ha were obtained in isolated areas c.f. the maximum sampled natural density of 0.07 pairs / ha.

III. The composition of breeding starling populations

The West Melton breeding population was comprised :

(a) birds which bred in the study area in successive years,

(b) birds which fledged in the study area, and

(c) birds of unknown origin.

(a) Birds which bred in the study area in successive years

Marked birds generally bred in the same colony (= a discrete group of boxes) and often in the same box each year. Of 235 adults banded at nests, 50 were recaptured 12 months later, and 11 of these recaptured for a third time, 12 months later still. Forty-nine birds of this sample bred in the same colony in both / all occasions; the remaining bird moved to the nearest colony 2.1 km away.

The recaptured sample included 46 females, 21 (46%) of which bred in the same site for two successive years, and four for three successive years. Only four males were recaptured, one at a different site. As males select the nest site (Marples, 1936; Kessel, 1957), their apparently greater site-fidelity seems reasonable.

Starlings apparently bred monogamously, and often retained their mates from year to year. Eleven pairs were banded but only two were recaptured. One partnership was unchanged and at the same site, but the other birds had changed mates; the male retaining the original nest site. In Holland, most birds mate anew each year (Kluijver, 1933). As birds of both sexes generally bred close to, if not in the site of the preceding year, the selection of new mates probably often results from the death of the old.

(b) Birds which fledged in the study area

Regrettably, only 8 (2.5%) nestlings (4 in 1970, 4 in 1971) were recaptured as breeding adults, all 24 months after fledging. One male and one female bred in their natal colonies but the other six (all females) were recaptured at different colonies (Fig. 6). The number of birds of similar history "expected" to breed in boxes about West Melton in 1970 was determined from a modification of Cave's (1968) formula viz.

$$N\ (t-2)\ t = \frac{N\ (t-2)}{n\ (t-2)} \times \frac{2\ Nt}{nt} \times n\ (t-2)\ t,$$

where $N\ (t-2)\ t$ = the number of nestlings fledged in the year

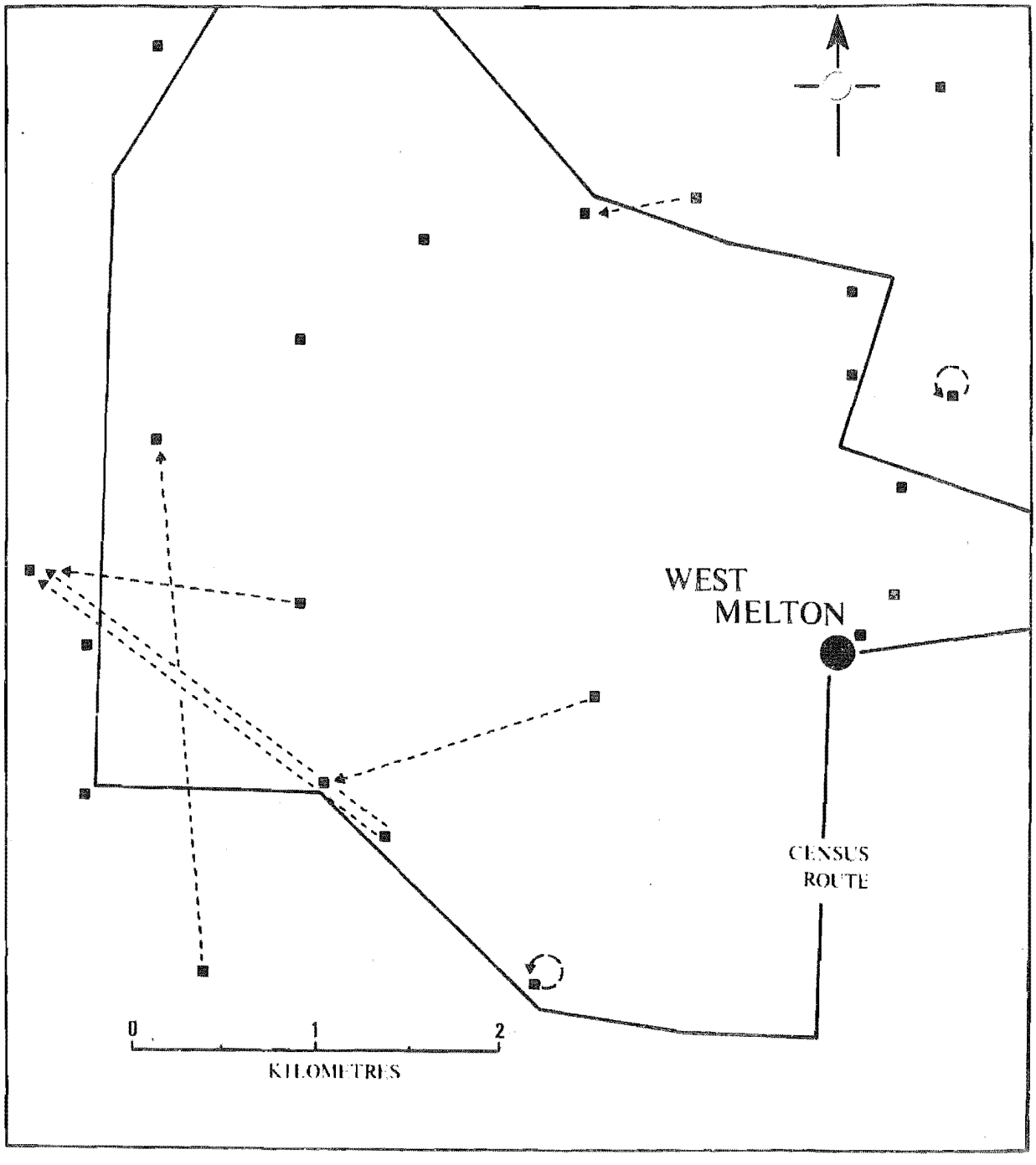

WEST
MELTON
CENSUS
ROUTE
0
1
2
KILOMETRES

Fig. 6

The movement of starlings about West Melton from their natal colonies to subsequent breeding sites. The solid squares indicate box colonies, the broken lines bird movements.

t - 2 (= 1968) and expected to be breeding in the year t (= 1970),

N (t - 2) = the number of nestlings fledged in the year t - 2,

n (t - 2) = the number of nestlings banded in the year t - 2,

Nt = the number of clutches laid in the year t,

nt = the number of breeding birds (both male and female) recaptured in the year t; and

n (t - 2) t = the number of fledglings banded in the year t - 2 and recaptured in the year t.

In the present study $N\ (t-2)\ t = \frac{108}{84} \times \frac{320}{66} \times 4 = \underline{\underline{9.9}}$ birds.

This calculation contains two inherent approximations, but neither seriously affects the figure obtained. The value for Nt (the number of clutches laid in 1968) may have been slightly high as a few birds laid in more than one nest site. Also, though unlikely, some birds may not have laid in their second year. Kessel (1957) considered that approximately 17% of fledglings survived to breed two years later c.f. 11.8% (9.9) of all fledglings from Canterbury nest boxes. Although Kessel's figure was an approximation, it appears that young starlings generally incur a high mortality in their first two years of life, move out of the study area, or both. From the recaptured sample the latter appears likely, at least in females, but remains unproven. Marked birds were never recorded outside the study area, but as banding returns from rural passerines are typically notoriously low (e.g. 1-4% for most British passerines; Thomson, 1964), undetected movements were possible.

(c) Birds of unknown origin

The unmarked starlings captured breeding may have been immigrants or have fledged from natural nest sites within the study area. Having once bred however, starlings rarely moved to other localities in subsequent years, and it appears likely that unmarked birds which occupied newly erected boxes, were of local origin and breeding for the first time.

IV. The age of breeding starlings

In November 1970, 73 breeding females were captured in boxes and aged. Of these, 26 had been banded as adults in the previous year and so were at least two years old (confirmed by hackle measurements); one (1.4 %) was probably one year old,

34 (46.6%) were two years or older, and 12 (16.4%) were of uncertain age. Concurrently, 20 breeding males were captured. Of these, three were banded while breeding in the previous year, but all 20 were considered to be two years old or more.

Nest boxes at West Melton frequently contained poorly constructed, incomplete nests, which were never laid in (Table 6). These incomplete nests were frequently made, destroyed and re-made by unpaired males, who typically carolled incessantly throughout much of the breeding season. A small number of unfinished nests may have been built by birds which died prior to egg laying, and others by birds which built a second nest adjacent to their first (Marples, 1936), but most were the work of celibate males.

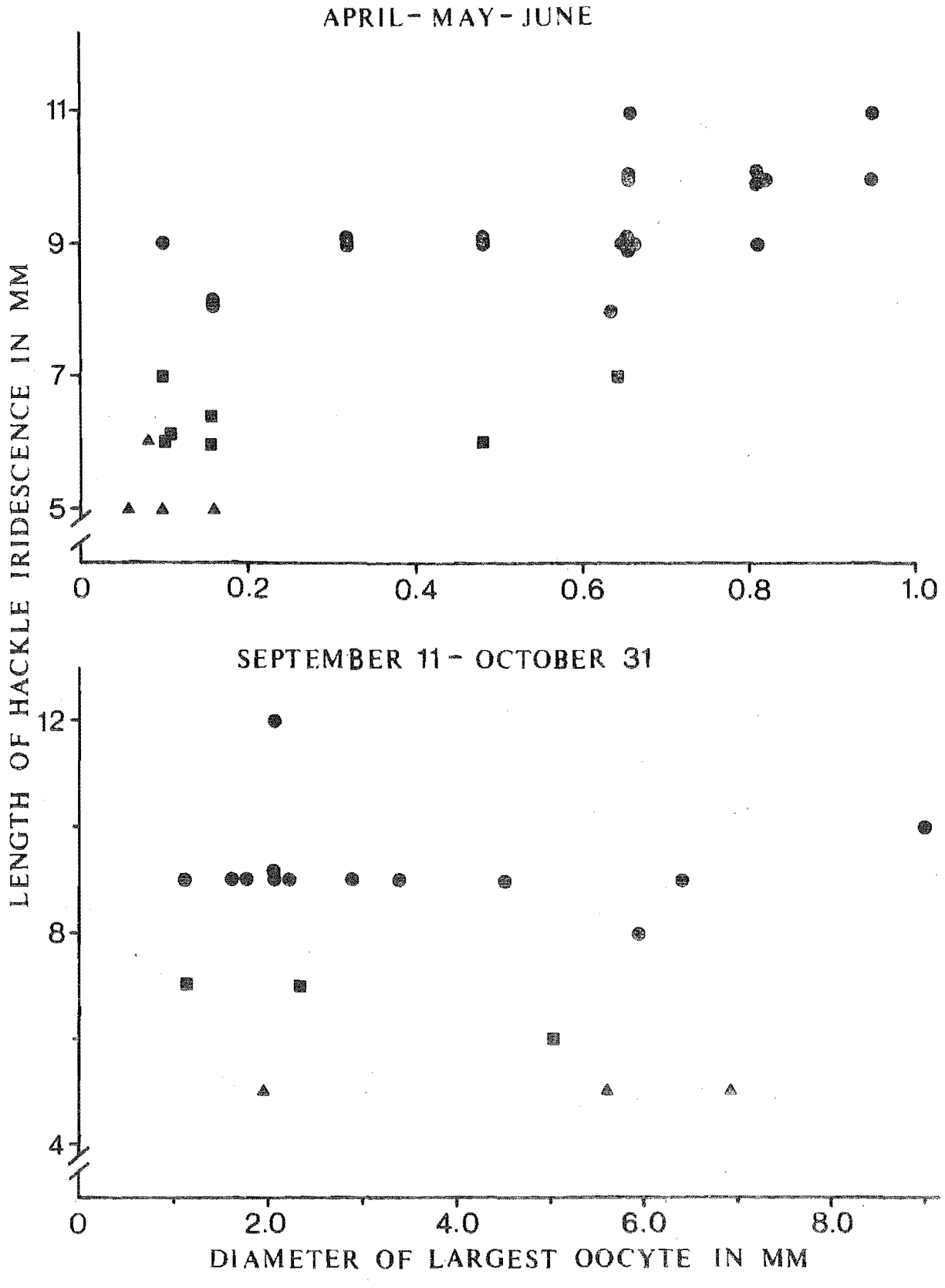
The age and reproductive capacity of free-flying starlings were indicated by gonad size. During winter, the size of the gonads in birds of both sexes was correlated with the iridescence of their throat hackles (Fig. 7, A & B; $r = 0.603$ for males and 0.762 for females, both significant at 0.01% level). During spring, the correlation coefficient (r) of these two variables again differed significantly from zero for males ($r = 0.423$, $p < 0.01$), but not for females. Thus in spring, all first year males or those of uncertain age (hackle groups A and B respectively, see Ch. 3.2.II) had smaller testes than adult birds and, like those in Britain (Bullough, 1942), probably did not breed. Conversely, some first year females and those of uncertain age (groups A or B respectively) had mature ovaries in spring and must have been part of the breeding population.

V. Territoriality and competition for nest sites

(a) Territoriality

The territory of the starling, being the area defended from competing conspecifics (Armstrong, 1947), was in Canterbury limited to the nest cavity and its immediate environs. Nest boxes were placed one metre apart in three localities in 1968, and subsequently only one box of each pair was occupied by starlings. Natural nest sites had similar territorial limits e.g. starlings bred in a disused railway siding near West Melton and built their nests on roof "rafters" 1.3 m apart, but never on members between the rafters. The territory was apparently

FEMALES A


APRIL - MAY - JUNE
LENGTH OF HACKLE IRIDESCENCE IN MM
11
9
7
5
0
0.2
0.4
0.6
0.8
1.0
SEPTEMBER 11 - OCTOBER 31
12
8
4
0
2.0
4.0
6.0
8.0
DIAMETER OF LARGEST OOCYTE IN MM

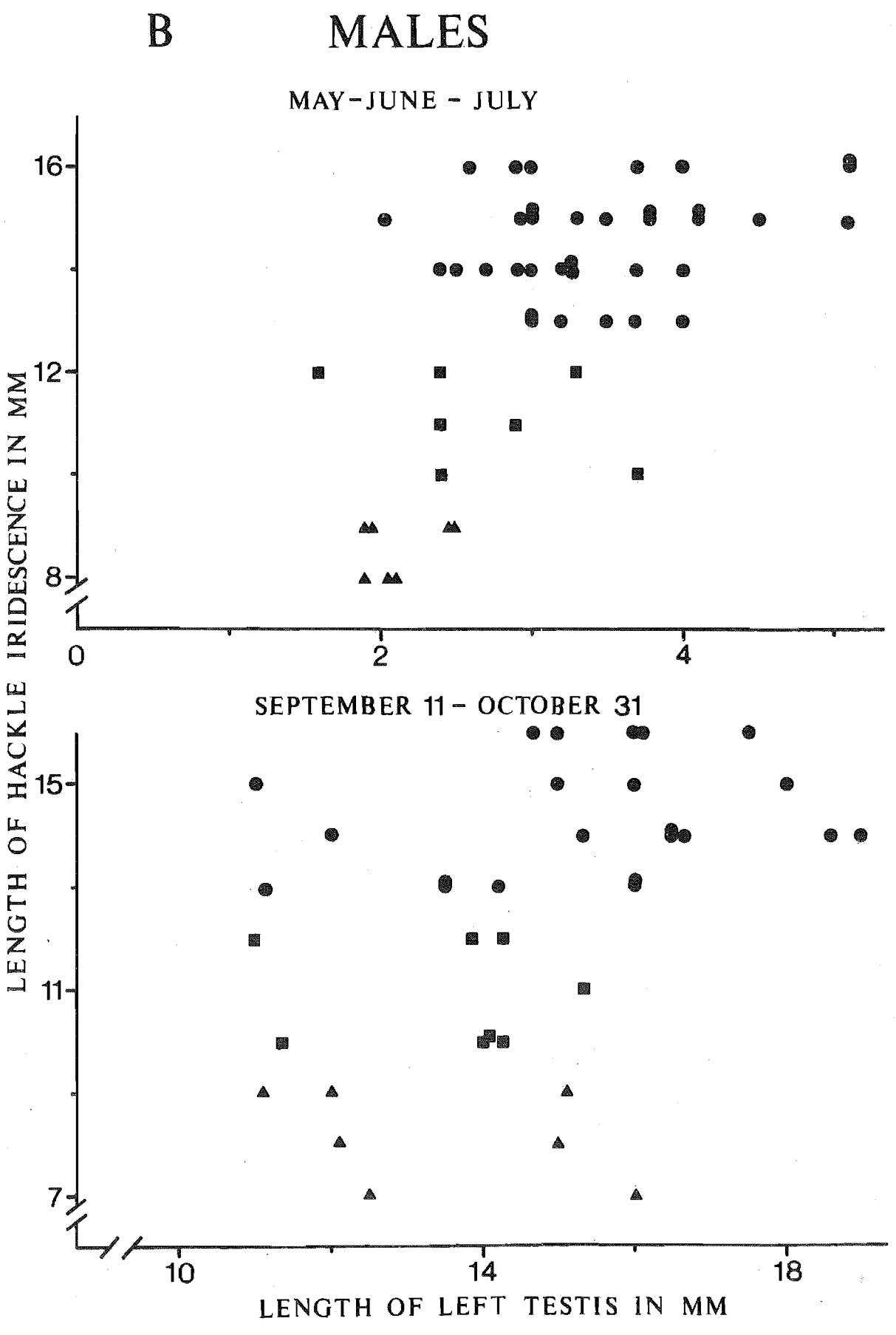

B
MALES
MAY-JUNE - JULY
16
12
8
0
2
4
SEPTEMBER 11 - OCTOBER 31
15
11
7
10
14
18
LENGTH OF HACKLE IRIDESCENCE IN MM
LENGTH OF LEFT TESTIS IN MM

Fig. 7, A & B.

The relationship between gonad size and hackle feather iridescence of male and female adult (●), indeterminate (■) and first year (▲) starlings. Significant correlations were obtained for males ($r = 0.603$) and females ($r = 0.762$) in winter but only for males in spring ($r = 0.423$).

limited to a sphere about the nest entrance, 60 to 100 cm in radius c.f. a sphere of 25 to 50 cm, Wallraff (1953); Kessel (1957).

(b) Competition for nest sites

(i) Intraspecific competition

Few nest sites remained unoccupied in any year (Table 6). Birds removed, and natural deserters, were rapidly replaced, apparently by birds about to breed for the first time e.g. on 28.10.69 a female which had just laid was shot, and a second female occupied the box and laid eight days later. In another instance, on 26.10.70 a box partly collapsed and was deserted immediately, but the owner was replaced by a new female who laid ten days later.

The ownership of sites and / or mates was frequently disputed between birds of the same sex, within the nest box especially in 1969 and 1970. Disputes occurred throughout the breeding season, and at all phases of the breeding cycle (Table 11). Male combatants were observed less frequently than females, largely because males selected sites earlier than females and at a time when my visits to the colonies were infrequent. Two males were found fighting in a nest site on one occasion, but as laying never followed they were probably one-year-old birds contesting a recently-deserted site. Disputes generally caused the destruction of eggs or nestlings present, and in one instance a banded adult female was found in its nest pecked to death and with its brain removed (also reported to occur in house sparrows, Passer domesticus, Summers-Smith, 1963).

Interference with nests, and the destruction of their contents was common. Unidentified birds were seen to fly from site to site, peer into each in turn and enter some. Breeding adults also visited other boxes; a marked hen with eggs of her own was found "incubating" a clutch laid by another bird in an adjacent site. Nest materials, eggs and nestlings were commonly found below nests, and the fatal pecking of nestlings was a frequent occurrence e.g. on 17.11.69 five vociferous adults flew in and out of a box which contained four severely-pecked dying nestlings.

Table 11. INTRASPECIFIC COMPETITION FOR NEST BOXES

Sex of combatants	Date	Stage of breeding	Result of conflict
F	12.8.69	nest selection	unknown- neither bird became the subsequent occupant
M	31.10.69	following egg laying	eggs destroyed- victor unknown- nest rebuilt
F	25.11.69	following fledging	no further use of box
F	23.11.69	" "	"
F	12.10.70	prior to egg laying	both combatants deserted- occupied by new bird
F	20.10.70	"	nest rebuilt
F	30.10.70	nestling period	brood destroyed- owner relaid
F	9.11.70	during incubation	clutch destroyed- owner relaid

(ii) Interspecific competition

Starlings competed for nest sites with house sparrows which occupied boxes between October and January (Table 12), but mostly in December (66.3%). Nest boxes occupied by sparrows in October and November were generally those unacceptable to starlings because of human disturbance or territorial strife.

Table 12. NEST BOX OCCUPATION BY HOUSE SPARROWS IN 1970

Time of occupation	Following starling occupation	In Unoccupied Boxes
October	-	2
November	2	10
December	59	-
January	17	-

House sparrows in Canterbury had three egg-laying periods which corresponded to their first, second and third clutches, and occurred in late October, late November to early December, and late December to early January respectively (Dawson, 1966). The sudden increase in box occupation by sparrows in early December preceded the laying of their third clutches. Although house sparrows, like starlings, are generally faithful to their nest sites, they prefer the protection of a cavity and vacate open natural sites when boxes are provided nearby (Summers-Smith, 1963).

House sparrows preferred nest boxes erected in hedgerows (55; 55.6% in 1970), to those on open fence lines (20; 23.5%). They congregate in breeding colonies, and tend to ignore nearby apparently suitable nesting sites (Summers-Smith, op.cit.). Because open fence lines did not normally provide nest sites for them, their colonization of boxes erected there was generally slow.

VI. Egg laying

(a) The timing of the breeding season

Canterbury starlings breed between mid-October and late December (Fig. 8). Breeding follows a gonadal recrudesence (period of growth) that begins in mid-winter (June) when temperatures are lowest, food supply variable and day-length the only constant environmental factor. Laying dates at West Melton vary significantly from year to year within narrow limits however, (see below) and the precise timing each year must be governed by some short-term factor rather than day-length.

Air temperatures early in October (October 1 - 10) affect the laying of Canterbury birds. Temperatures were significantly lower in 1969 than in 1970, but not 1968 ($H = 4.325$, $p < 0.05$; $H = 2.895$, $0.1 > p > 0.05$ respectively). Eggs of first clutches were laid significantly earlier in 1968 and 1970 than in 1969 ($H = 62.507$, $p < 0.001$; $H = 39.169$, $p < 0.001$, respectively), and also significantly earlier in 1968 than in 1970 ($H = 5.804$, $p < 0.05$), but temperatures prior to laying in the latter years were similar.

(b) The gonad cycle

The gonads of adult starlings underwent an annual cycle

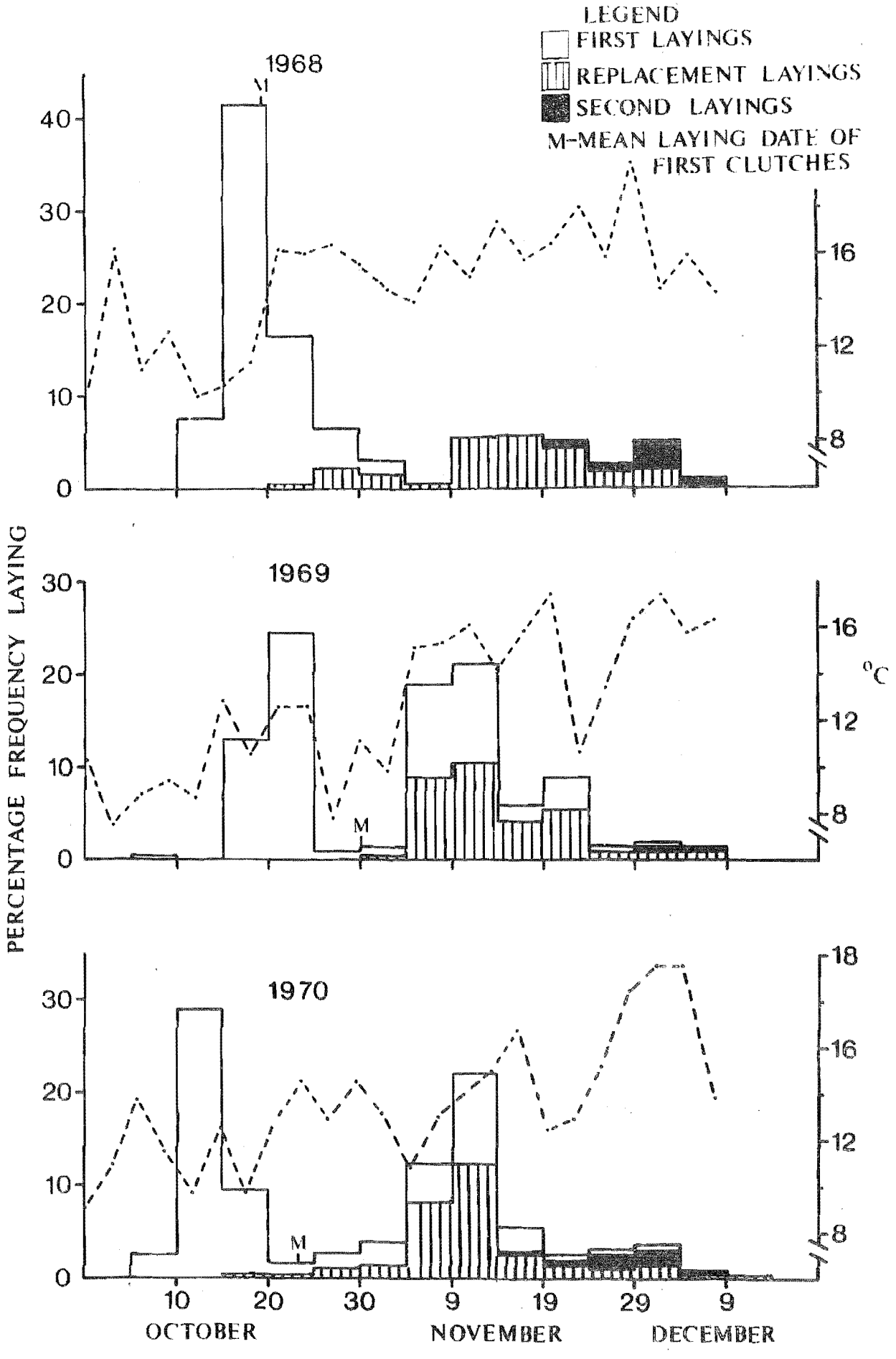

LEGEND
FIRST LAYINGS
REPLACEMENT LAYINGS
SECOND LAYINGS
M-MEAN LAYING DATE OF FIRST CLUTCHES
1968
1969
1970
M
PERCENTAGE FREQUENCY LAYING
°C
0
10
20
30
40
8
12
16
18
10
20
30
9
19
29
9
OCTOBER
NOVEMBER
DECEMBER

Fig. 8

Laying histograms of starlings at West Melton. Data obtained from 67 pairs in 1968, 143 in 1969 and 160 in 1970. Concurrent mean daily temperatures (daily maximum / 2 + daily minimum / 2) are also shown.

of development which closely followed yearly temperature regimes (Fig. 9). They were smallest in March and April (testis length = 2.8 ± 0.10 mm, ovarian follicle diameter = 0.38 ± 0.052 mm), and largest in October (the start of laying) e.g. testis length = 14.6 ± 0.35 mm, ovarian follicle diameter = 5.49 ± 1.038 mm. Females collected in October at Harewood had ovaries with follicles up to 12.6 mm in diameter; an ovulable size.

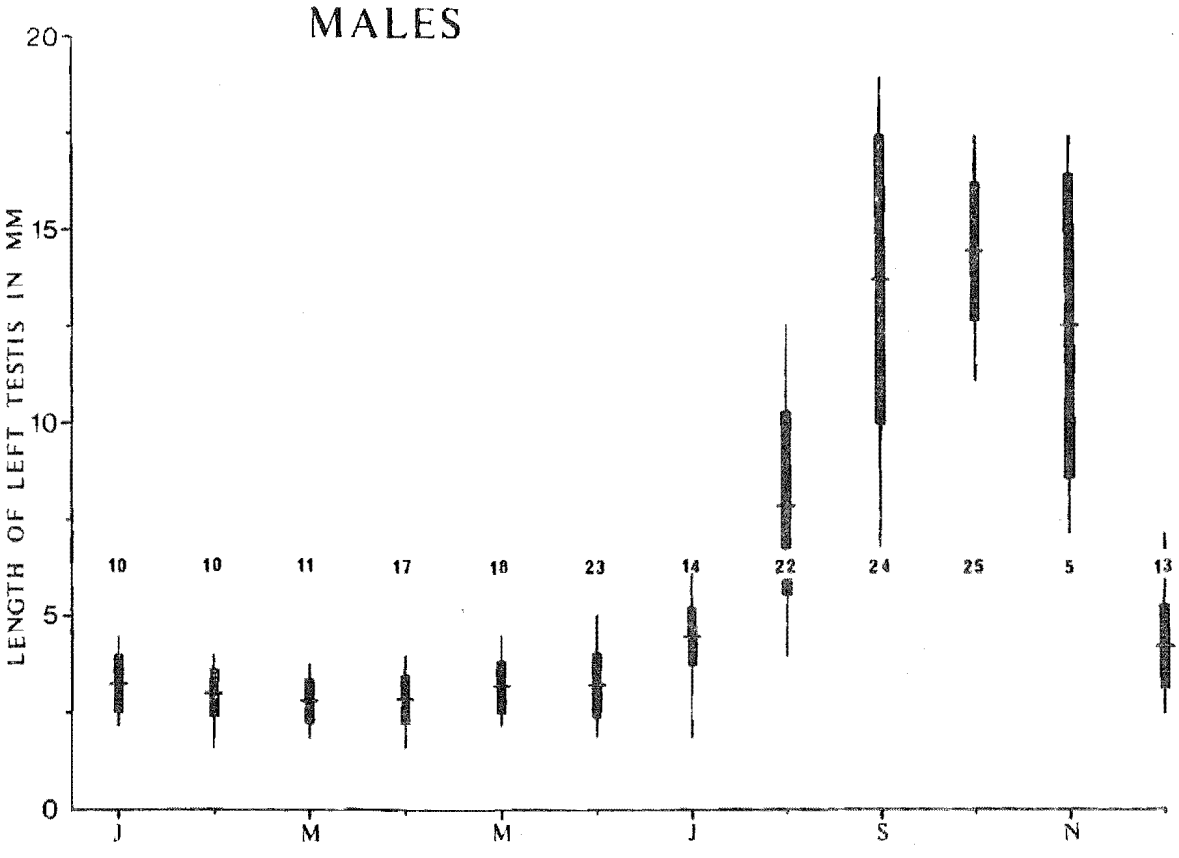
Commencement of gonad recrudescence coincided with the appearance of breeding plumage and concomitant sexual activity. Following breeding, testes and ovaries rapidly regressed (returned to a non-breeding state) and sexual activity decreased markedly. Although the data are limited, the gonads of birds in juvenile plumage showed similar trends i.e. they regressed following fledging but recrudesced before spring.

(c) Laying

Starlings laid at West Melton between October 8 and December 11 (Fig. 8). Laying patterns were trimodal; the first and second modes were separated by three to four weeks, and the second and third modes by approximately three. The first mode represented eggs derived largely from first clutches, whereas the second and third modes were a result of the combined effect of first, replacement and second clutches. Many starlings lost clutches, but often replaced them within two weeks (8 days was the minimal replacement time recorded). Second layings followed the fledging of successful first broods, with successive layings five to six weeks apart.

The synchrony of first layings determined the kurtic nature of the second and third laying modes. In 1969 and 1970 the second mode was more leptokurtic (peaked) than in 1968, as in the later years many replacement clutches were laid concurrently with a number of late first clutches. In 1969, initial laying was interrupted by inclement weather, particularly by low temperatures (Fig. 8). Reasons for the bimodal nature of first layings in 1970 were not evident. In 1968, first layings were more restricted, with all (62) clutches started within 17 days (S.D. = 3.9) of the beginning of laying c.f. S.D's. of 1.0 to 1.9 days recorded from 20 to 67 first clutches laid in Scotland between 1950 and 1956 (Anderson, 1961).

Females generally laid single eggs on successive days


MALES
LENGTH OF LEFT TESTIS IN MM
20
15
10
5
0
10
10
11
17
18
23
14
22
24
25
5
13
J
M
M
J
S
N

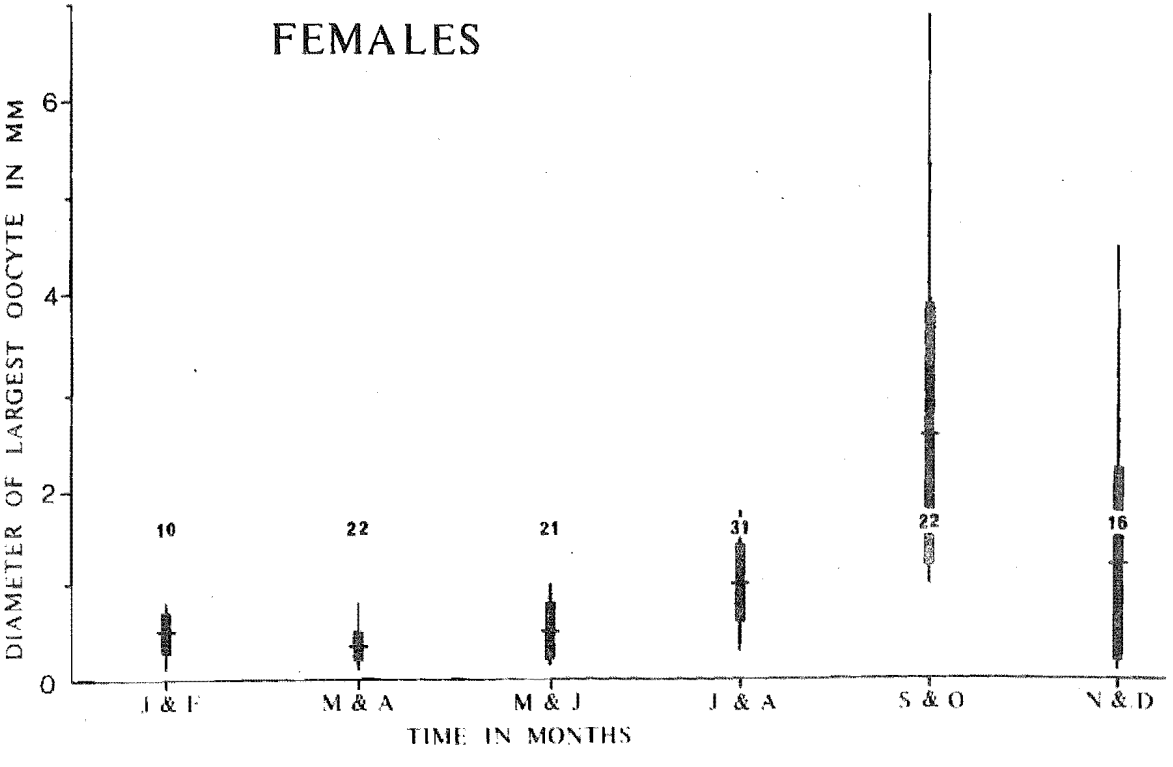

FEMALES
DIAMETER OF LARGEST OOCYTE IN MM
6
4
2
0
10
22
21
31
22
16
J & F
M & A
M & J
J & A
S & O
N & D
TIME IN MONTHS

Fig. 9

Seasonal variations in gonad dimensions of adult male and female starlings. Each monthly or bimonthly entry is represented by a mean (the horizontal line), one standard deviation (S.D.) on either side of the mean (the solid bar), a range (the vertical line) and a sample size.

until clutches were complete. However, 20 irregular layings followed the last eggs of first clutches, with time lags of 11.65± 0.888 days (5.98% of all first clutches). They were laid during the incubation and early nestling period of preceding clutches but, being out of phase, failed to produce young. Irregular layings emphasised the indeterminate nature of the starlings' laying, with their absence following later layings probably resulting from a physiological slowing down in the rate of conversion of food into egg material. Kessel (1957) recorded one irregular laying (in 301 clutches), but summarily dismissed it as laid by another female. Canterbury birds infrequently left their nests unguarded during the incubation period, and conspecific nest parasitism on a scale needed to account for the irregular layings seems unlikely.

(d) The effect of age on the time of laying

The laying dates of 24 females were known for two successive years. In 1969, these birds laid concurrently with the rest of the population, but in 1970 significantly earlier ($H = 4.455$, $p < 0.05$). In 1969, the mean age of the sample was apparently representative of the total population, but was older one year later, when all the marked birds were breeding for at least the second time. Similar age - laying date relationships have been recorded for starlings in Holland (Kluijver, 1933) and Belgium (Verheyen, 1969b).

(e) Clutch size

The clutch size of Canterbury starlings ranged from two to eight eggs, with the frequency of each size varying annually, and with successive replacement or second layings. Overall, clutches of 3, 4 and 5 occurred most frequently, clutches of 2 and 6 infrequently and clutches of 1, 7 and 8 rarely.

Single layings preceded 9.2% of first clutches. They generally followed the capture of pre-laying females and, with two exceptions, were lost immediately. Others may have been laid during the infrequent visits made to nest sites by neighbouring adults. As single eggs were of doubtful parental origin, they, along with part-clutches lost during laying, have been excluded from subsequent determinations.

(f) Factors affecting the size of first clutches

The average size of first clutches varied from year to year, with those laid in 1968 being significantly larger than

clutches laid in 1969 ($H = 9.148$, $p < 0.001$) or 1970 ($H = 4.706$, $p < 0.05$; Table 13). Clutches laid in 1969 and 1970 were not significantly different.

TABLE 13. AVERAGE CLUTCH SIZE OF STARLINGS IN CANTERBURY

Nature of Laying	1968 N.	1968 Mean	1968 S.E.	1969 N.	1969 Mean	1969 S.E.	1970 N.	1970 Mean	1970 S.E.
First	62	4.39	0.147	121	3.90	0.101	141	4.10	0.091
Second	7	3.14	0.242	2	3.00	0.000	14	3.79	0.207
First replacement	18	4.00	0.248	41	4.15	0.171	46	4.41	0.159
Second replacement	-	-	-	3	3.67	-	5	3.00	0.632

Clutch size was affected by the age of the breeding hen. Fourteen marked birds of unknown age averaged significantly smaller clutches in 1969 (4.00 ± 0.335) than in 1970, when one year older (4.50 ± 0.167; t adj = 2.941, $p < 0.05$). Of these, five laid identical sized clutches in both years, with seven laying larger and two smaller clutches in the latter year.

(g) Subsequent layings

The frequency of second and replacement layings varied annually (Table 13). In 1968, second clutches followed first clutches more frequently (11.3%) and replacement clutches less frequently (29.0%) than in any other year. Conversely, in 1969 second clutches were rare (1.7%) but replacement clutches more common (33.9%). Data from 1970 were intermediate. Similar annual variations in the frequency of these layings were noted by Kluijver (1933), Creutz (1939), and Havlin and Folk (1961).

Starlings laid significantly smaller second (3.14 ± 0.242 eggs) than first clutches in 1968 (4.39 ± 0.147 eggs; $H = 8.174$, $p < 0.001$; Table 13). A scarcity of second clutches in 1969 curtailed analysis, while in 1970 differences were not significant. The size of first and replacement clutches was similar in all years studied.

VII. Breeding success

(a) Mortality in the nest

(i) Egg losses

The nature and frequency of natural egg losses from first, second and replacement clutches were similar (Tables 14 & 15 respectively). Unnatural losses were attributable to investigator disturbance.

Table 14. LOSSES OF EGGS AND NESTLINGS FROM FIRST CLUTCHES AND BROODS

Reason for loss	Time of Loss																				
	Following laying			Mid incubation			Late incubation			At hatching			Following hatching (days) 0 - 5			6 - 14			15 - 22		
	68	69	70*	68	69	70	68	69	70	68	69	70	68	69	70	68	69	70	68	69	70
Box failure		6							4									4		4	
Predation					3	4			7							13	4			1	
Intraspecific fighting	1	2	11		7	5		2					2	2	18	2	5	11	2		
Unhatched										15	36	70									
Buried in the nest						5															
Disappeared	18	56	24	9	21	20	11	4	3	24	8	80	42	44	54	27	25	47		1	
Starved													1	2	8	4	6	13		1	5
Human disturbance															3		10				

Note: Table excludes losses resulting directly from the author's activities

* 68, 69, & 70 = 1968, 1969, 1970

Table 15. LOSSES OF EGGS AND NESTLINGS FROM SECOND AND REPLACEMENT CLUTCHES AND BROODS

Reason for loss	Time of Loss																				
	Following laying			Mid incubation			Late incubation			At hatching			Following hatching (days) 0 - 5			6 - 14			15 - 22		
	68	69	70*	68	69	70	68	69	70	68	69	70	68	69	70	68	69	70	68	69	70
Box failure			1			9															
Predation				2		7			5								7				
Intraspecific fighting	1		2		4	9							3	7	1	2	1	13		4	
Unhatched										3	25	24									
Buried in the nest									3												
Disappeared	18	15	21	8	5	21	1		4	40	15	82	4	34	19	10	11	29			
Starved														5	6		12	1		4	
Human disturbance																	8				
Deserted						5															

Note: Table excludes losses resulting directly from the author's activities
* 68, 69, 70 indicates 1968, 1969 and 1970

In first clutches (Table 14), most natural losses (61%) were recorded as 'disappeared', and occurred immediately following laying, or at the end of the incubation period. As 21% of remaining losses were of unhatched eggs, probably many of those which disappeared after complete incubation also suffered physiological failure.

Eggs were lost during intraspecific fights (6.1%) within the nest and occurred even when the resident bird managed to rout the transgressor. Less frequently, and independently of the stage of incubation, losses were due to nest-box failure (2.2%), burial in the nest lining (1.1%) and mammalian predation (3.1%).

The losses of entire clutches resulted from box failure, predation, or intraspecific fighting, and single eggs from their burial or physiological failure. The frequency and causes of egg losses were similar each year, except for those following intraspecific fighting. In 1968, nest ownership was rarely disputed, but in subsequent years disputes and egg losses occurred with increasing frequency (see Ch. 5.3.V), as local populations became established and competition for nest sites increased.

(ii) Nestling losses

Mortality factors of nestlings and eggs were similar (Tables 14 & 15). Natural losses of nestlings were similar in nature and frequency in all types of broods (Table 14), with most successful broods incurring some mortality (e.g. only 20.9% of first broods were wholly successful).

In first broods, most losses (66.5%) occurred when nestlings disappeared. These were generally entire broods lost during early or mid-nestling periods, either from intraspecific fighting or mammalian predation. During intraspecific fighting, nestlings were pecked about the head and thorax and thrown out of the box by the parent or transgressor. Stoats were seen eating nestlings on two occasions, and attacked mainly those aged five to ten days (5.6%), when they were most vociferous.

Many nestlings (11.1%) died from starvation. Generally, they were intermediate-aged last-hatched nestlings who, being smaller than their siblings, competed less successfully for food. Nestlings of deserted broods died from attendant chilling, as much as from starvation. Occasional losses

followed the failure of boxes (2.2%) and interference by children (3.6%).

(b) Breeding success

The breeding success of successful first clutches (viz. those which fledged one or more nestlings) laid in 1968 was significantly greater than in 1969 or 1970 (Table 16). Breeding success for 1969 and 1970 and hatching success in all years was similar.

Hatching success (eggs hatched / eggs laid) was independent of clutch size, but the number of nestlings hatched per pair was greater in larger clutches and broods of four and five occurred frequently. Breeding success (nestlings fledged / eggs laid) was generally greatest for the modal clutch sizes viz. 3, 4 and 5, but in some years clutches of six and seven fledged more nestlings. Overall, the mean number of nestlings fledged from first broods ranged from 2.45 $\pm$ 0.050 in 1969 to 3.01 $\pm$ 0.117 in 1968, and breeding success from 59.97 $\pm$ 1.034% in 1969 to 68.42 $\pm$ 1.075% in 1968 c.f. a value of 83% obtained for starlings in North America (Kessel, 1957).

Successful second broods occurred infrequently and although their breeding success was similar to that of successful first broods (72% for seven broods laid in 1968 and 1970), they contributed little towards the overall productivity of the population. Replacement broods were also of little consequence as they rarely fledged young, and those that did had lower success than normal broods e.g. a maximum 56% success was recorded in 1968.

4. DISCUSSION

I. Natural and artificial populations

Starlings in rural Canterbury build their nests in cavities in farm buildings and rarely in trees. Increases in local populations at West Melton were obtained by providing artificial sites, as farm buildings occur sporadically and suitable sites are few. Starlings have been similarly established or increased elsewhere in the world, and it appears that the lack of suitable nest cavities commonly limits their breeding populations e.g. in North America (Kessel, 1957;

Table 16. BREEDING SUCCESS OF THE FIRST LAYINGS OF STARLINGS AT WEST MELTON

Clutch size	No. of Clutches	Hatching success	Ave. no. hatched/pair	Breeding success	Ave. no. fledged/pair
			1968		
2	2	100.0	2.0	50.0	1.0
3	3	100.0	3.0	77.8	2.3
4	10	92.5	3.7	70.0	2.8
5	15	80.0	4.0	69.3	3.5
6	2	91.7	5.5	58.3	3.5
Mean	4.37	87.53	3.78	68.42	3.01
			1969		
3	9	85.2	2.6	70.4	2.1
4	27	75.9	3.0	59.3	2.4
5	9	84.4	4.2	57.8	2.9
6	2	83.3	5.0	33.3	2.0
7	1	100.0	7.0	57.1	4.0
Mean	4.15	80.05	3.32	59.97	2.45
			1970		
2	1	100.0	2.0	100.0	2.0
3	7	90.5	2.7	81.0	2.4
4	17	70.6	2.8	64.7	2.6
5	16	80.0	4.0	60.0	3.0
6	3	61.1	3.7	44.4	2.7
7	1	100.0	7.0	28.6	2.0
8	1	100.0	8.0	25.0	2.0
Mean	4.43	78.20	3.45	63.34	2.68

Breeding Success

1968 & 1969 $t = 14.271$, $p < 0.001$

1968 & 1970 $t_{adj} = 2.345$, $p < 0.05$

1969 & 1970 $t_{adj} = 1.570$, n.s.

Royall, 1966), Scotland (Anderson, 1961) and Czechoslovakia (Hudec and Folk, 1961). In North-West Germany, starling numbers have recently increased significantly due to local building programmes providing suitable sites (Oelke, 1967). Local increases of many other cavity-nesters have been obtained through the provision of nest sites e.g. pied flycatcher Muscicapa hypoleuca (Von Haartman, 1957; Voous, 1960), kestrel Falco tinnunculus (Cave, 1968), grey starling Sturnus cineraceous (Kurodo, 1959), myna Acridotheres tristis (Akhmedov, 1957) and numerous cavity-nesters in Britain (Williamson, 1968).

Artificial sites erected near perching stations or foraging areas are occupied first, as they are most easily located. Hedgerow boxes are used more frequently than those on open fence-lines or near human dwellings.

II. The age and origins of breeding birds

Canterbury starlings generally breed first when aged two, although a few precocious females breed when aged one. Males are physiologically incapable of breeding at one, although sometimes they occupy sites and display vigorously. First year female breeders, but not males, are common in many countries e.g. Holland (Kluijver, 1933), Belgium (Verheyen, 1969b) and North America (Collins and DeVos, 1966), although both are rare in others e.g. Latvia (Vilks and Transehe, 1933).

Breeding follows gonadal maturation which apparently can be inhibited by an inadequate diet (Bissonette, 1933). In Canterbury, during all but final maturation, first year birds carry relatively less body fat than mature ones (see Ch. 8.3) and must have greater difficulty in coming into breeding condition, apparently because they feed less successfully (see Ch. 6.3.IV). One-year old males may be prevented from breeding by the starlings monogamous mating system acting in association with an excess of males, which according to Kluijver (op.cit.) limits social interactions and ultimately the maturation of courtship displays. Male magpies, Pica pica, mature at one but do not breed until the following year, apparently for the same reasons (Erpino, 1969).

Like starlings in Holland (Kluijver, 1933) and North America (Kessel, 1957), Canterbury birds breed in the same area and often the same site each year. Fledglings generally,

but not always, breed away from their natal colony. Most birds which occupy boxes in new "box-colonies" are breeding for the first time and are committed to them in subsequent years.

III. Competition for nest sites

Most of the nest boxes used are occupied by starlings each year. Their suitability for this species has one drawback; there is a severe annual intraspecific and limited interspecific competition of individual sites. Both are features common to many hole-nesting bird species (Von Haartman, 1957).

Males generally select nest sites and mates one month or more before laying begins (Kluijver, 1933; Marples, 1936; Cohen, 1951) although unattached Canterbury birds of either sex often obtain both at a later date by vigorous fights with mated resident birds. However, other species which breed monogamously or pair for life generally show only limited competition for mates (Sibley, 1957), and much of the overt aggression amongst Canterbury birds is probably directed towards obtaining a nest site.

Overt aggression within nests by adults often reduces breeding success. One-year males have on occasion been blamed for most nest depredations e.g. Wallraff (1953) and Kessel (1957), although Kluijver (1938) believed that young males frequently assist in the feeding of nearby young. Similar competition has led to reduced breeding success in populations of grey starlings (Kurodo, 1964) and wood ducks Aix sponsa (Jones and Leopold, 1967).

House sparrows frequently occupy nest boxes following the fledging or failure of starlings' first broods. Although one former resident attempted to parasitize a nest built subsequently by a sparrow, the smaller species generally appears able to limit the laying of the larger bird. House sparrows in Southern Russia successfully occupy the boxes of mynas, their bulky nests apparently forming suitable barriers against attacks by the larger bird (Akhmedov, 1957).

IV. The timing of breeding

Air temperatures determine the precise laying dates of many bird species, either directly through the retardation of

final ovulation, or indirectly through food e.g. Marshall, 1949; Lack, 1954, 1966; Owen, 1959; Cave, 1968. Laying dates of local starlings are determined by air temperatures with final ovulation being retarded by cold. Laying of starlings in North America (Kessel, 1957; Royall, 1966) and Scotland (Dunnet, 1955) is similarly delayed.

Late spring air temperatures in Canterbury do not appear to determine laying dates through the regulation of invertebrate food species, as the nature of the latter largely remained unchanged prior to and during early breeding (determined from adult gizzard contents and nestling "collar samples"). The occurrence of major starling foods in Scotland does not change significantly at this time of year (Dunnet, 1955).

Gonad maturation follows an annual cycle of development and determines the appearance of breeding plumage and sexual activity. Gonad growth is maximal in the month preceding laying and, as suggested for the ring dove Streptopelia risoria (Lehrman, 1965) and zebra finch Poephila guttata (Butterfield, 1970), apparently results from the constant presence of a mate and associated changes in social life.

V. Laying

Canterbury starlings lay between mid-October and mid-December. Laying patterns are influenced by inclement weather, the age of breeding birds and the time of fledging or loss of first and successive broods. Low temperatures during laying (i.e. in 1969) lead to temporary cessations, with similar restraints shown by golden plover Charadrius apricarius (Rowan, 1918), fieldfare Turdus pilaris (Pitt, 1929) and several other Turdus species (Myres, 1955). Conversely, in a mild spring starlings tend to lay earlier and lay larger clutches. Parallel responses are shown by many species e.g. starlings in Germany, (Creutz, 1939) and kestrels in Holland (Cave, 1968).

On average older birds lay larger clutches and lay earlier in the season than first year breeders (also shown by Kluijver, 1935; Lack, 1948). It was therefore surprising that the average clutch size laid in 1968 in newly erected boxes was significantly larger than in 1969, especially as starlings tenaciously retain their nest sites from year to year. However, double the number of boxes was present in 1969 and the average

clutch size laid in boxes present both years was similar ($H = 3.860$, $0.05 > p > 0.01$).

Second and replacement clutches follow the fledging of first broods or the failure of first layings respectively. Second clutches are laid near the end of the laying period and are commonest in years of early laying e.g. 1968. They only follow clutches laid earliest and if lost are not replaced (e.g. after 11.3% of first clutches in 1968 c.f. 93% of early broods in North America (Kessel, 1957)). Conversely, replacement clutches follow losses of any clutches, whenever laid, and may themselves be replaced if lost. They occur most frequently when laying is delayed by inclement weather e.g. 1969.

Canterbury clutches average from 3.9 to 4.4 eggs and are smaller than those recorded in other countries, apparently due to differences in latitude (see Lack, 1947) e.g. clutch size in Holland = 5.3 (N = 1592), Kluijver, 1933; England 4.9 (N = 105), Lack, 1948; Scotland 5.1 (N = 106), Dunnet, 1955; New York 5.5 (N = 199), Kessel, 1957.

VI. Brood statistics and breeding success

Nestlings remain in the nest for approximately 22 days. Brood sizes at hatching range from one to eight but at fledging are rarely larger than four.

Most egg and nestling losses occurred during intra-specific fighting. Others were lost to mammalian predators, especially intermediate-aged nestlings, and others because of nest box failure. A few eggs / nestlings were lost at hatching, apparently following physiological failure.

Breeding success is greatest in first broods and, of these, is generally maximal for the commonest clutch sizes i.e. 3, 4 and 5; the latter fledging 2.1 to 3.5 nestlings per brood each year. Second and replacement broods occur infrequently, have a lower rate of success, fledge fewer nestlings, and contribute little towards the overall productivity of the population.

In summary, in years when pre-laying temperatures are mild and starlings lay earlier than usual (viz. 1968), they lay larger first clutches and more frequent second clutches, have larger first broods, higher hatching and fledging success and eventually fledge more nestlings. Conversely, in years in which the spring climate is less favourable and the species

lays later (viz. 1969), birds produce smaller clutches and broods, fledge fewer nestlings, and have a lower breeding success. At the same time second clutches are rarer but replacement clutches more common.

CHAPTER 6

THE FOODS AND FEEDING OF STARLINGS

1. INTRODUCTION

The diverse diet of starlings in rural areas of New Zealand and other countries has resulted in disagreement over whether their activities are beneficial or detrimental to mans' agricultural interests. Although there is an extensive literature on the diet of starlings (see Ch. 1), for an assessment of the species economic importance in rural Mid-Canterbury local evaluation of its feeding ecology was necessary. For this purpose, foraging movements and methods of feeding and selection of feeding sites were examined about local roosts and breeding sites. Simultaneously, the diets of adults and nestlings were investigated; the diet of nestlings is important, for when they are present starlings prey heavily on particular invertebrates selected for their size, texture or palatability.

2. METHODS

I. Roost observations

Knowledge of the location of communal roosts, and hence the daily origins of feeding flocks, permitted estimates to be made of foraging ranges. Roosts were located by following the flight lines of birds leaving or entering them, while the positions of others were already known by local farmers. In addition, 50 nest boxes were checked at night once a month for roosting birds.

II. Feeding habits

The diet of any animal is determined by its selection of feeding sites. At West Melton, feeding sites (= field preferences) and starling numbers over 777 ha (106 fields) were determined once a week, from January 1969 to March 1970 inclusive, by driving over a 21.17 km standardized census route. Each census began at 1000 hr and took approximately six hours to complete. Halts were made at field boundaries and beside

larger fields and the adjoining areas scanned with 8 x 60 or 16 x 50 binoculars. Birds feeding in short-grazed pasture were readily counted, but those in rank pasture or tall crops were "put up" for counting by sounding the automobile horn.

Starling field preferences were analysed using techniques outlined by Dunnet and Patterson (1970) and a computer programme written by S.M. Robson of this department. An index of the utilization of field types (= I.U.) was determined from the ratio between the percentage of all starlings seen on a particular field form and the percentage occurrence of that field form in the area censused. Index values of less than unity showed an avoidance by birds, of greater than unity a positive selection and of unity a lack of either.

Field selection and foraging ranges were interdependent. The latter were delimited about roosts by the sighting or collection of marked birds at feeding sites. During breeding, foraging ranges were determined by direct observations, made from hides, of birds travelling to and from nest sites.

Feeding actions and the form of flocks on a variety of foods and feeding grounds were also determined by field observation. Generally an automobile was used as a mobile hide and birds were often approached to within 40 m in this way.

Food selection by caged starlings was examined during digestion experiments (for a detailed account of methods, see Ch. 7.2). When 41 adult and first year males and females were fed mixed meals of common foods, any species specifically rejected were noted. No attempt was made to place items randomly in feeding dishes as most were alive and active. Studies of food selectivity in the field involved numeric comparisons of the major foods eaten by feeding groups of four to eight birds, with the invertebrates obtained from 20 soil samples taken at the same site immediately afterwards. The latter, measuring 12 cm in diameter and 6 cm in depth were taken at exact sites chosen from a table of random numbers (Fisher and Yates, 1948), and the invertebrates present collected by washing the soil over a 180 micron sieve and drying the turf in Tullgren extractors.

III. The diet

The diet of starlings at West Melton was largely

determined from examination of the gizzard contents of birds shot after more than an hour of feeding on any one field. Efforts were made to collect 40 birds per month between 1000 and 1500 hr daily throughout the year. Smaller samples in November and December were supplemented by foods collected from nestlings with the aid of feeding collars (see Kluijver, 1933), and prey obtained in this way was whole and easy to identify and count. Samples were collected simultaneously from all members of individual broods and from nestlings of all age groups. Collars were kept on for up to an hour, but no chick was robbed of food more frequently than every third day. In all, 199 and 98 individual samples, each consisting of several "meals", were collected in 1969 and 1970 respectively, and a further 80 nestling gizzards were collected in 1971.

Shot birds were immediately given an oesophageal injection of 1 cc of 10% formalin to arrest post-mortem digestion (see Van Koersveld, 1951; Dillery, 1965), and later frozen after approximately three hours at ambient temperatures. Subsequently, each gizzard sample was searched microscopically for earthworm setae, then washed on a 180 micron "Endecott" sieve and sorted under a variable-power stereoscopic microscope. Unidentified foods were catalogued (see Morgans, 1965) and later checked against reference material. Invertebrate foods were quantitatively recorded using total numbers and percentage occurrence techniques, determined from quantifiable remains such as head capsules, abdomens, paired elytra or wings. Each method complemented the other and when used together eliminated much of the bias normally associated with such numerical methodology (see Hartley, 1948). Cereal remains were estimated volumetrically by spot-count methods (see Poore, 1969), as partly-digested plant material rendered numerical techniques inadequate (Hartley, op.cit.).

The size and frequency of nestling meals were determined from the recorded frequency of parental visits to nestlings and on examination of foods collected after individual parental visits.

The nutrient value of major foods taken by adults and nestlings was determined by calorimetry. Twenty (>0.01 g dry weight) or 50 (<0.01 g dry weight) individuals of each species, depending on average size, were dried to constant

weight in a vacuum oven at 65° C. Samples were finely ground and sub-samples of approximately 0.2 g made into a pellet and burnt in oxygen in the combustion chamber of a "Parr" semimicro-calorimeter. Subsequent methods followed those outlined by the Parr company (1960) and gave heats of combustion for each sample burnt. Calorimetric reproducibility was checked with five burnings of earthworms whose heats of combustion ranged from 5.20 to 5.68 Cal /g and averaged 5.36 ± 0.2 Cal /g ash-free dry weight.

The average amount of chitin present in each species burnt was also determined, as chitin is indigestible to vertebrates (Stiven, 1961) and is a common element of starling faeces. Methods followed those outlined by Fraenkel and Rudall (1947). Samples identical to those mentioned above were boiled in alkali (Potassium hydroxide) for 24 hr in a reflux condenser. Chemical action was subsequently arrested by neutralizing the remaining tissue in 1% Hydrochloric acid for 5 min and later washing in distilled water for 30 min, before taking the sample to constant weight. Caloric values for chitin in each species (determined as 5.69 Cal /g) were then subtracted from the calculated heats of combustion and a value for the energy content of "digestible tissues" obtained. Finally, the total caloric value of each major species ingested was calculated by multiplying the value determined for "digestible" tissues by the number of each species recorded from gizzard or nestling food samples. Such values are, however, slightly high; Stiven (op.cit.) reported that approximately 80% of ingested digestible tissues are absorbed, the remainder (20%) being lost in gaseous, urinary or faecal wastes. The fraction is apparently approximately constant for most arthropods and correction factors have not been added in this study.

3. RESULTS

I. Feeding activities

(a) Daily patterns and feeding ranges

In the non-breeding period, roosts are deserted each day immediately before or at sunrise, as birds move out in various-sized flocks (depending largely on roost size) to feeding sites. On the way, vacated breeding cavities are generally

Plate 3

Flock feeding of starlings. Small flocks often fed in association with stock but large ones rarely.

(Photographs - H.A. Best)

visited where, even in winter when foraging time is short, birds may spend up to 2 hr in comfort activities and singing. Sometimes, similar activities occur during the day at temporary roosting sites adjacent to feeding areas. Starlings begin moving back to roosts approximately 1 hr before sunset. Nest cavities are again visited and desultory feeding may occur nearby. At sunset, birds rapidly enter roosts, although in autumn spectacular pre-roosting aerial displays often occur.

Foraging ranges about West Melton roosts extended up to 4 km in mid-winter but were considerably less at other times. In the non-breeding period, starlings always moved to the nearest communal roost each night and no area within the census route was greater than 4 km from any roost (see Fig. 4). The foraging areas of flocks from neighbouring roosts probably did not overlap (also recorded by Wynne-Edwards, 1931) as adults (and often associated first year birds) radiated out to feed about their own deserted breeding-sites each day.

(b) Flock displays

Starlings generally feed communally, rarely on their own. Feeding flocks are usually species-specific and although other birds such as house sparrows and gulls may feed with starlings, they do not form an integral part of the parent flock.

Flock size varies seasonally (Fig. 10). During breeding, starlings commonly forage in groups of less than 10 and rarely in numbers greater than 30. At other times, small flocks (< 20) are still dominant but larger ones of 50 to 100 birds occur frequently and 100 to 500 occasionally.

Small flocks generally forage alongside occupied or vacated nest sites. Members feed quietly one to two metres apart, moving slowly and independently of their neighbours (Plate 3). They are commonly associated with stock, particularly sheep (Fig. 11), using their backs as observation posts for predator detection and their feet as "beaters" of invertebrates (also recorded for some birds in North America e.g. cowbirds - Melothrus ater and starlings, Forbush, 1927; ravens - Corvus corax, Bent, 1946; ani - Crotophaga sulcirostris, Rand, 1953). During breeding, small flocks are characterized by birds ferrying back and forth between feeding and nest sites. At other times aerial movements are irregular

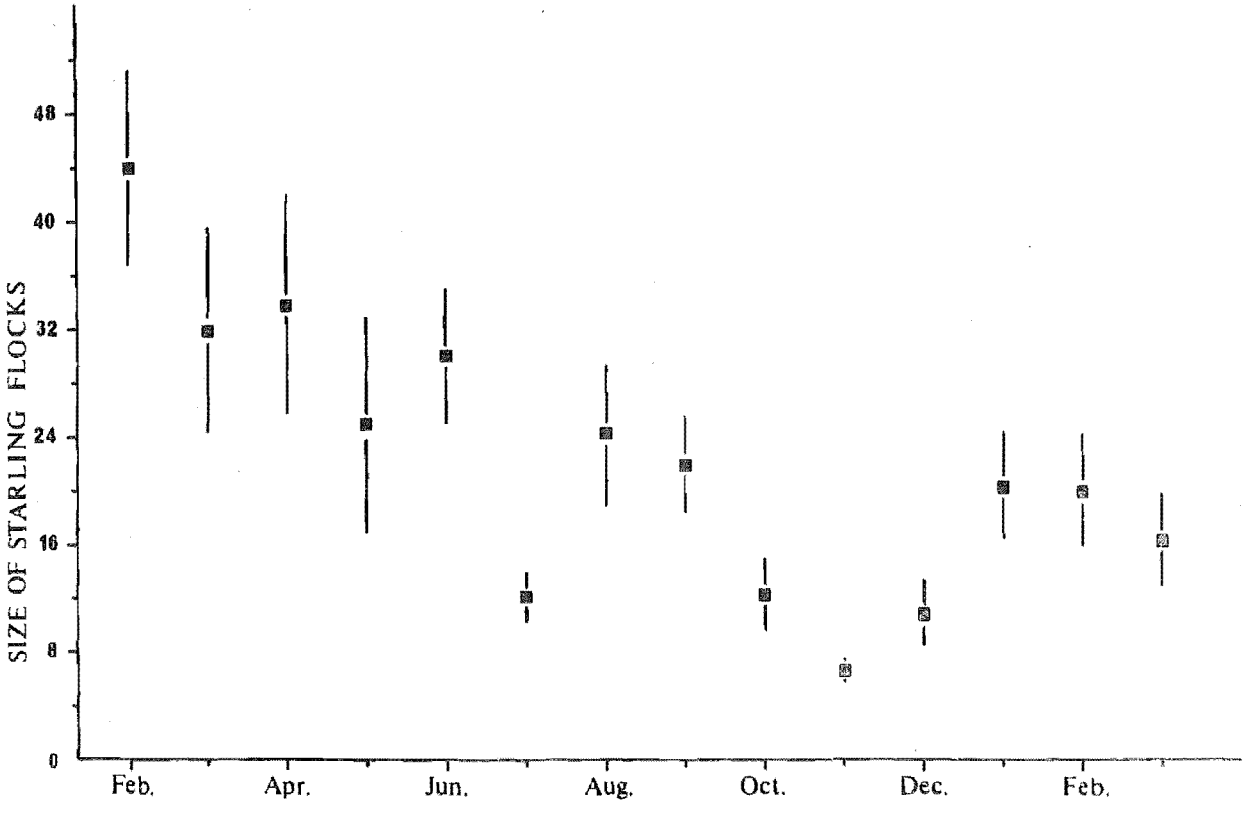

SIZE OF STARLING FLOCKS
48
40
32
24
16
8
0
Feb.
Apr.
Jun.
Aug.
Oct.
Dec.
Feb.

Fig. 10

Seasonal variation in the flock size of feeding starlings. The mean and standard error are given for each sample.

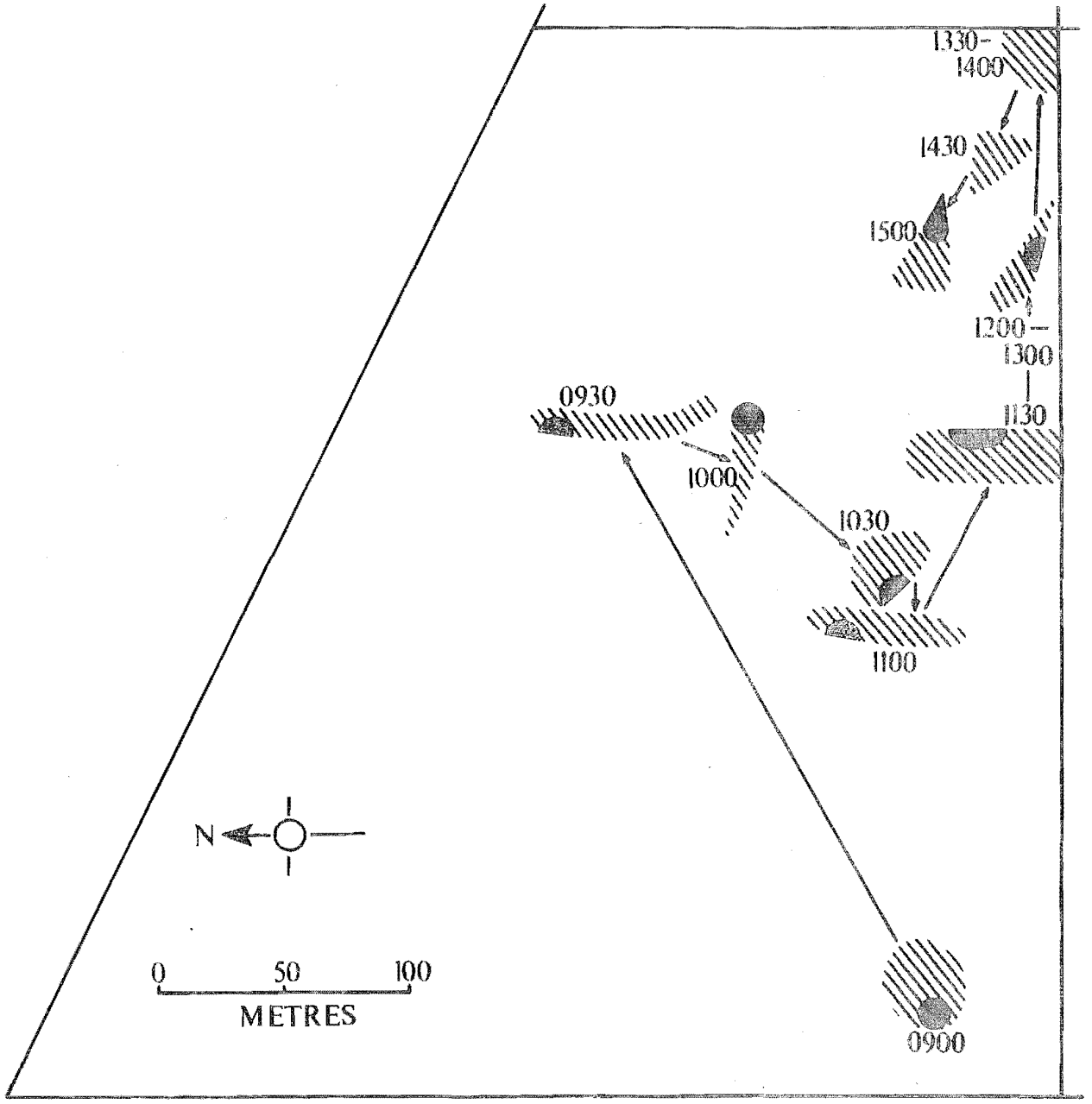

1330–
1400
1430
1500
1200–
1300
1130
0930
1000
1030
1100
0900
N
0
50
100
METRES

Fig. 11

The association of a starling flock (40 birds - solid area) with sheep (50 - hatched area) on a field in West Melton. Observation times and directions of movement are also shown. Note that the birds fed amongst the stock during all but a period of roosting shortly after midday.

and only follow alarms, when the flock moves en masse to nearby roosting trees for protection and comfort activities. Small flocks have small foraging ranges and probably consist predominantly of birds which once bred nearby; one out of two marked adults shot in the non-breeding period (28.1.70) was collected alongside (400 m away) its old nest site.

During late summer, autumn and winter large flocks of 100 to 500 starlings occur frequently, and members differ markedly in their behaviour from those in smaller flocks. In large flocks, birds become closely integrated with their neighbours through social facilitation (see Hinde, 1961) and often feed within pecking distance; this is apparently because mutual attraction overcomes normal spatial adjustments resulting from aggression (Emlen, 1952). Members are noisy and typically move rapidly and in one direction across fields in "roller feeding" fashion, similar to that described for weavers - Quelea quelea (Ward, 1965). Birds stop momentarily with food and drift to the rear; they then break off and fly over the group to drop down in front of advancing birds. The flock thus undergoes a continual change of leadership. Large flocks are occasionally joined by small neighbouring groups, apparently through local enhancement (see Turner, 1964).

(c) Parental feeding behaviour

Nestling foods were gathered by parents in fields near the nest and regurgitated directly into the gapes of begging nestlings. Parents rarely returned to the nest without food. Once the chicks were homiothermic (3-4 days after hatching, Kluijver, 1938) females apparently foraged more frequently than males; 22 out of 30 (74%) visits recorded in $4\frac{1}{2}$ hr at one nest site were by the hen. Similar divisions of labour were recorded by Kluijver (1933) and Kessel (1957).

During the nestling period, parents were observed foraging only on pasture (as recorded in Scotland, Anderson, 1961) and the nestlings' foods consisted entirely of pastoral species of invertebrates. Starlings observed on other field types during the breeding season were probably non-breeders.

Starlings changed feeding sites frequently, there being no maintenance of feeding territories although birds often successively returned to one particular area in a field (Fig. 12). Grazing stock attracted loose groups of foraging

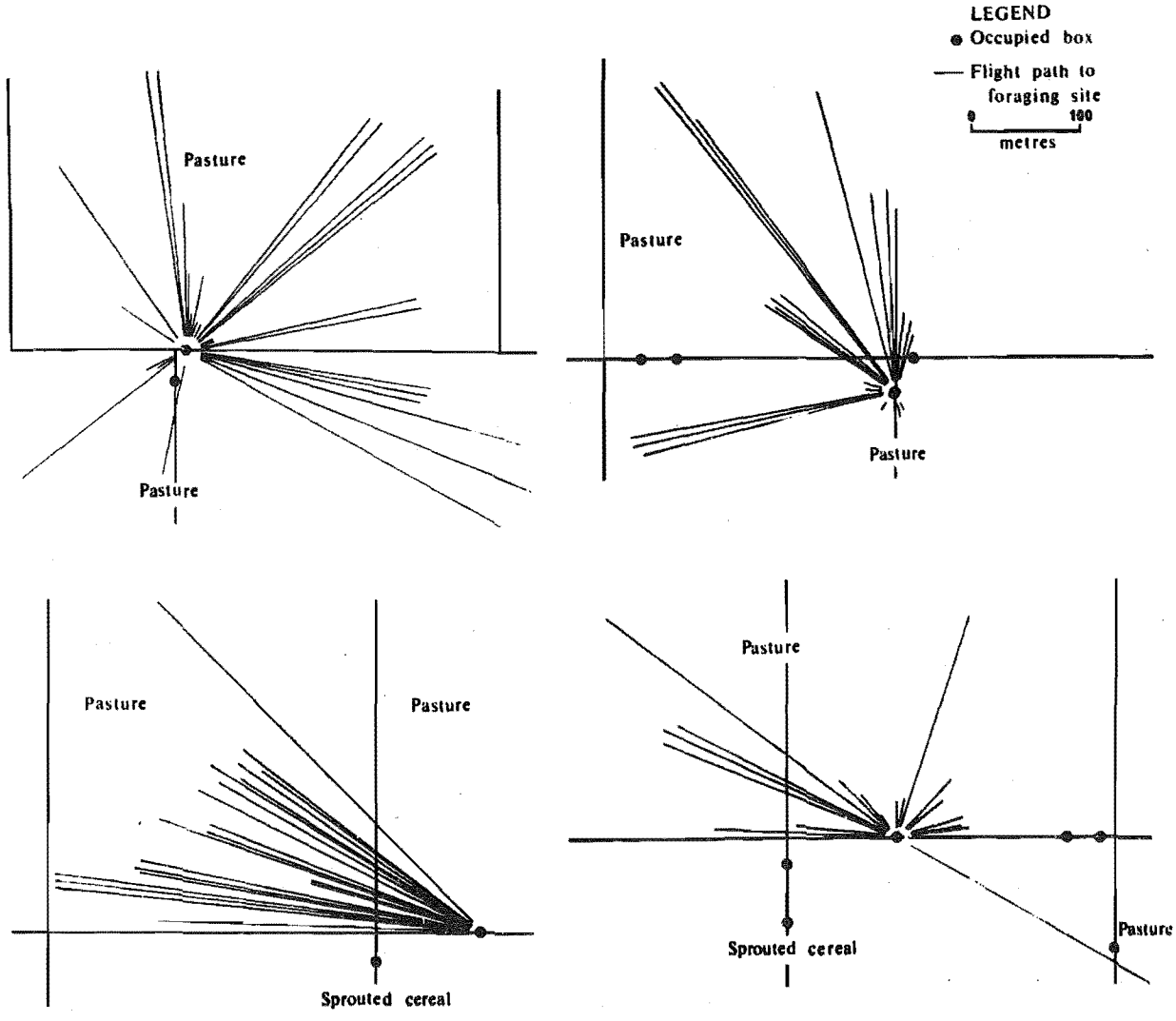

LEGEND
Occupied box
Flight path to foraging site
0
100
metres
Pasture
Pasture
Pasture
Pasture
Pasture
Pasture
Sprouted cereal
Pasture
Sprouted cereal

Fig. 12

Consecutive foraging ranges of parent birds recorded about four nest sites at West Melton. Note the avoidance of fields of sprouted cereal and the frequent return to the same foraging site.

birds and feeding sites changed with random stock movements.

Adults foraged up to 500 m away from nest sites, with mean values for four pairs ranging from 108 ± 18.8 m to 246 ± 31.5 m (Fig. 12).

(d) Feeding actions

The feeding actions of starlings are similar to those of corvids (see Lockie, 1956) and are determined by flock form and the nature and occurrence of foods. Actions common to all birds but characteristic of those in large flocks include:

(i) Pecking and / or surface probing - a common action whereby foods are picked up from the ground or surface sward, often following rummaging. Invertebrates "beaten" by neighbouring starlings or stock are captured in this way as are foods such as cereal grain and seeds.

(ii) Arboreal pecking - similar to (i) above, but used for foods on elevated crop foliage, especially brassicas e.g. turnips and choumoellier.

Feeding actions confined largely to birds foraging in small flocks include:

(i) Probing - vigorous bill-thrusting into small crevices and holes to enlarge them for subsequent visual search (called "zirkeln" by Lorenz, 1949). Probing is used frequently in spring and autumn on moist pasture soils, but not during frosty or dry conditions. In moist soils, starlings probe the length of their bill (approximately 25 mm), but do not exchange probing for digging actions like corvids (Lockie, op.cit.); invertebrates at depths of greater than 25 mm generally being unobtainable.

(ii) Dung - turning - the "billing" and overturning of dry stock dung followed by an inspection of its undersurface and of the turf beneath. Dung-turning occurs frequently in summer when dung is inhabited primarily by Diptera (especially Sarcophaga milleri) and numerous beetles. In this and other seasons, moist dung is also examined; the birds probing to extract prey.

(iii) Jumping - an action used to collect aerial foods. Jumping is infrequent and apparently confined to mid-summer when Diptera are particularly common. However, many flies and other flying forms such as Hemiptera and Lepidoptera are generally taken within the sward.

(iiii) Pouncing - a common extension of jumping; the bird leaping forward instead of upward at a distant prey.

II. Selectivity of feeding sites and food

(a) Occurrence of crop and field types

The nature of the fields censused (see Fig. 13) varied throughout the year depending on farming practices. Pasture was dominant (between 68 and 80%), with short-grazed grass (sward < 5 cm) common (approximately 80%) and long grass (< 12%) and lucerne (< 8%) less so. Fodder crops consisted largely of spring-sown turnips (< 12%) maturing in autumn, with rank "fodder" cereal and lupins less common. Barley, wheat, and oats (approximately 10%) occurred in some form or other throughout the year, being sown in autumn and spring, harvested in summer, and remaining stubble throughout winter. Potatoes and peas, the only other cash crops censused, occurred infrequently (< 3%) and were confined to warmer months. Fields frequently lay fallow throughout the year (< 21%), especially in early summer following peak cultivation in spring. Stock, particularly sheep, occurred on approximately 10% of fields censused and were confined to pasture, fodder crops and stubbles.

(b) Field selectivity

Feeding starlings show distinct preferences (i.e. I.U. > 1) for particular field types (Figs. 14 - 16). They select grass pasture in all but early winter (March to June) and generally avoid lucerne (Fig. 14, A & B); the selection of both in mid-winter results from their frequent use as cereal feed-lots for stock. Short-grazed pasture is consistently selected throughout the warmer months and the fields of longer herbage occasionally (Fig. 14, C - E). Preferences are influenced by stock, and in their absence both field types are avoided.

Starlings generally avoid cereal fields but do visit them in autumn when stubbles are most frequent (Fig. 15, A). Fields of sprouted and mature cereal are ignored, although rank cereal used as stock fodder in late winter attracts birds (Fig. 15, B). Stubbles are selected by birds from mid-summer to early winter, but only when stock are present (Fig. 15, C).

Fields of turnips are selected as feeding sites during

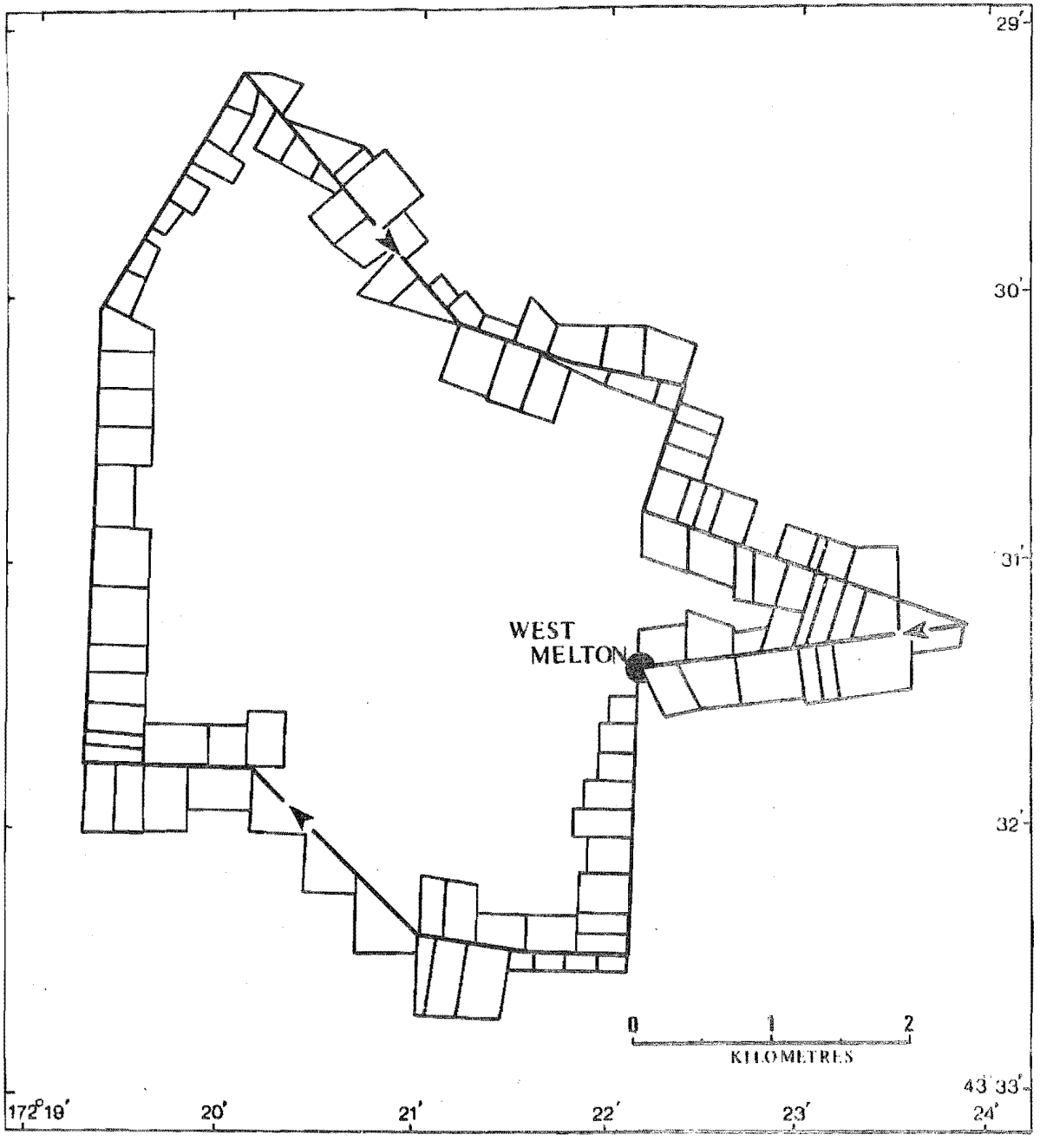

29'
30'
31'
32'
WEST
MELTON
0
1
2
KILOMETRES
43°33'
172°19'
20'
21'
22'
23'
24'

Fig. 13

The route travelled and fields censused for crops and starlings each week about West Melton.

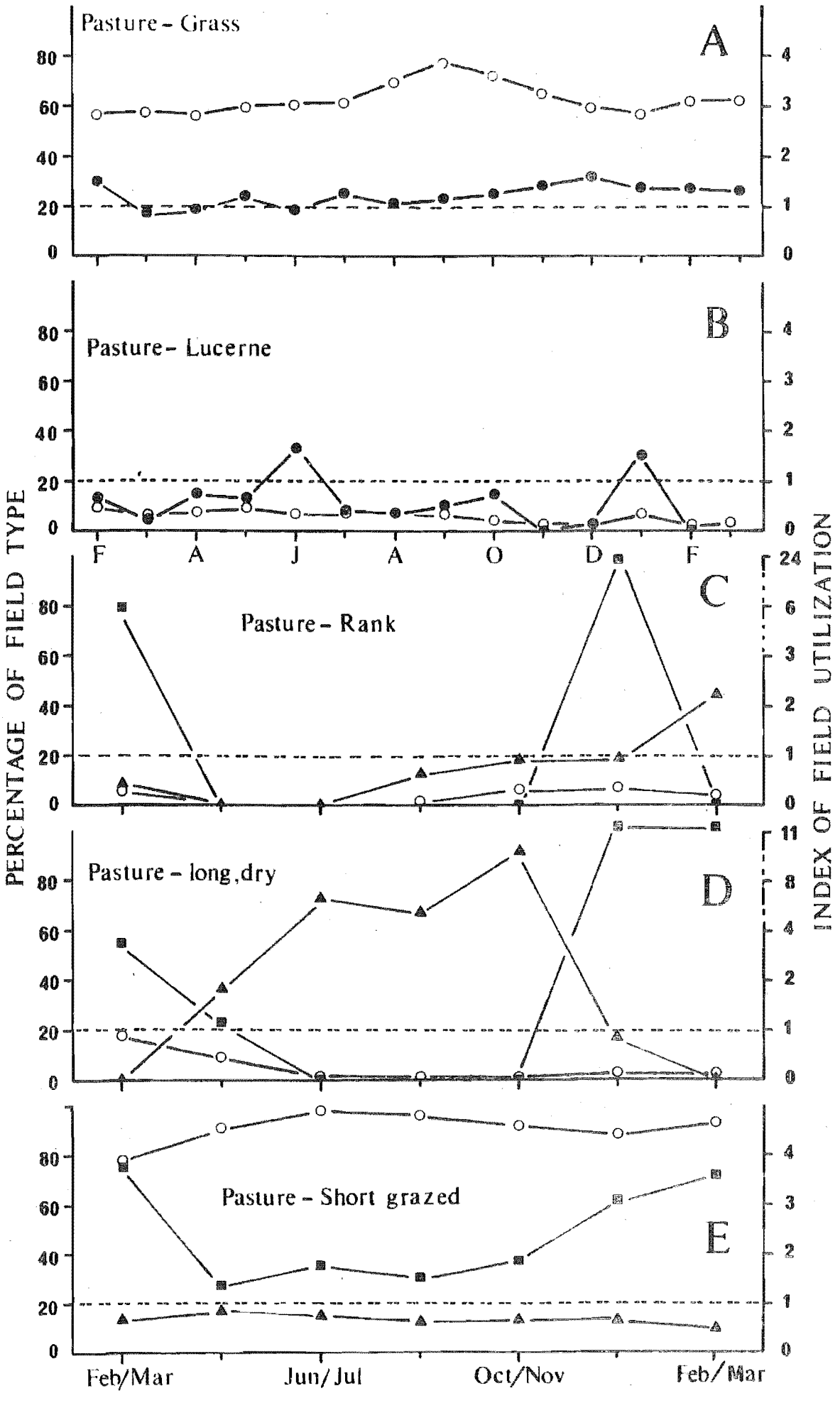

Pasture - Grass
A
Pasture - Lucerne
B
Pasture - Rank
C
Pasture - long, dry
D
Pasture - Short grazed
E
PERCENTAGE OF FIELD TYPE
INDEX OF FIELD UTILIZATION
F
A
J
A
O
D
F
Feb/Mar
Jun/Jul
Oct/Nov
Feb/Mar

Fig. 14

The selection of pasture fields by starlings. Percentages of pasture in the total area surveyed (A & B) and occupied by different pasture categories (C - E) are indicated by open circles for gass and lucerne and for rank, long-dry and short-grazed pasture respectively. Overall I.U. values and those recorded in the presence and absence of stock are indicated by closed circles, squares and triangles respectively.

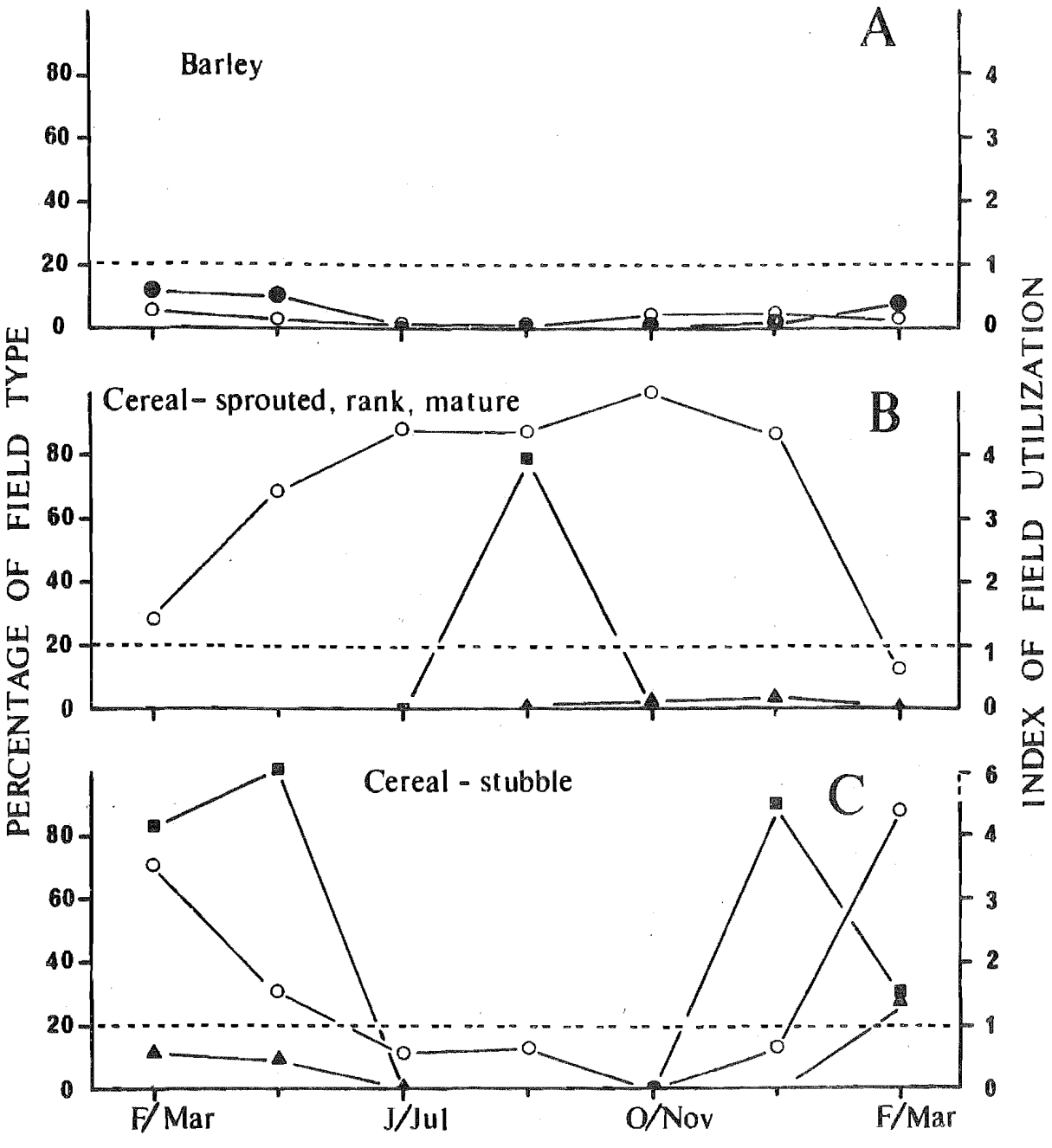

A
Barley
B
Cereal- sprouted, rank, mature
C
Cereal - stubble
PERCENTAGE OF FIELD TYPE
INDEX OF FIELD UTILIZATION
0
20
40
60
80
0
1
2
3
4
6
F/ Mar
J/Jul
O/Nov
F/Mar

Fig. 15

The selection of cereal fields by starlings. Barley covered more than 50% of all cereal surveyed and was indicative of trends shown for oats and wheat. The percentage of barley in the total area surveyed (A) and of different cereal stages in the area occupied by cereal (B & C) is indicated by open circles. Overall I.U. values and those recorded in the presence and absence of stock are indicated by closed circles, squares and triangles respectively.

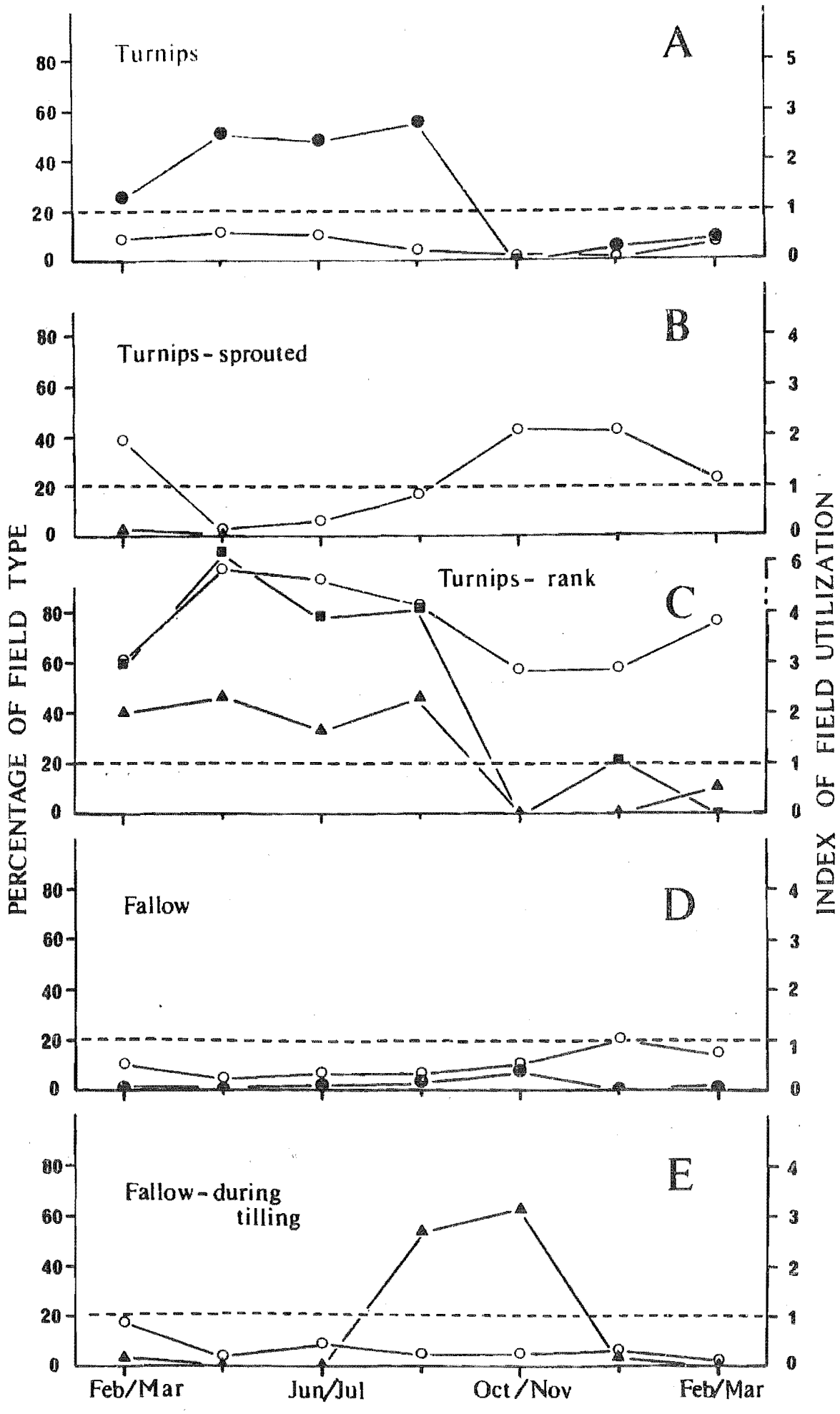

Turnips
A
Turnips - sprouted
B
Turnips - rank
C
Fallow
D
Fallow - during tilling
E
PERCENTAGE OF FIELD TYPE
INDEX OF FIELD UTILIZATION
Feb/Mar
Jun/Jul
Oct/Nov
Feb/Mar

Fig. 16

The selection of turnips and fallow fields by starlings. The percentage of turnips or fallow land in the total area surveyed (A & D) and of stages of turnip maturation and tilling in the area occupied by these field forms (B, C & E), is indicated by open circles. Overall I.U. values and those recorded in the presence and absence of stock are indicated by closed circles, squares and triangles respectively.

autumn, winter and early spring (Fig. 16, A), but are avoided in warmer months. Birds avoid fields of sprouted turnips (Fig. 16, B) but select those of rank turnips whether stock is present or not (Fig. 16, C).

Starlings rarely feed on fallow fields (Fig. 16, D). Selection occurs during spring tilling when starlings, along with gulls and rooks, "follow the plough" (Fig. 16, E). The presence of stock is then inconsequential. Birds never feed on potatoes and peas.

(c) Food selectivity

Changes in the feeding sites and hunting behaviour of starlings resulted in part from inherent food preferences. Such preferences were shown by caged starlings who, when presented with mixed meals of common foods (Table 17), selectively ate all soft-bodied larvae and spiders present. Adult beetles and flies were apparently less acceptable, with earthworms, Coleophora spp., Coccinella undecimpunctata and cereal even less so; the latter often ignored. An avoidance of coccinellid beetles seems entirely reasonable, as Imms (1957) reported that many members of this family are poisonous to vertebrates.

In the field, evidence of food selectivity by starlings was conflictive. The results of five analyses of invertebrate numbers taken by birds and in pastoral soil cores taken from their feeding sites were -

(1): Tau	= 0.2440,	$0.5 > p > 0.1$	n.s.	No. of birds = 4
(2): Tau	= 0.7379,	$0.1 > p > 0.05$	n.s.	" 6
(3): Tau	= 0.6671,	$0.05 > p > 0.01$	*	" 7
(4): Tau	= 0.8744,	$0.01 > p > 0.001$	**	" 8
(5): Tau	= 0.2108,	$0.5 > p > 0.1$	n.s.	" 5

where Tau = Kendall's coefficient of rank correlation (see Seigal, 1956).

Other fields were sampled after starling collection but the resultant soil cores contained too few invertebrate species for detailed comparisons. On occasion (samples 3 & 4), birds appeared to take foods locally most abundant, but as this was not universal e.g. samples 1, 2, 5, other factors must be involved. Even so, the major foods taken by starlings at West Melton agreed closely with the levels of natural abundance of the same revealed through intensive sampling at Harewood (see

Moeed, 1970), and the ease of capture of foods was obviously a decisive factor in starling feeding ecology.

Table 17. FOOD SELECTIVITY OF 41* CAGED STARLINGS

Food species		No. of items offered	No. eaten	Selectivity^{o}
Costelytra zealandica	L.$^{+}$	82	82	1.000
Tenebrio sp.	L.	82	82	1.000
Muscidae gen.undet.	L.	82	82	1.000
Lycosidae " "		82	82	1.000
Costelytra zealandica	A.$^{+}$	82	76	0.927
Muscidae gen. undet.	A.	82	76	0.927
Tenebrio sp.	A.	82	75	0.915
Apion ulicis		164	132	0.805
Lumbricidae gen.undet.		82	47	0.573
Coleophora sp.		164	79	0.482
Coccinella undecimpunctata		10	4	0.400
Cereal grain		82	31	0.378

Note:- Selectivity ^{o} = Number of food items eaten / number offered.

- * Coccinella undecimpunctata was presented to only 10 birds.
- L.$^{+}$, A.$^{+}$ = Larva and Adult stages respectively.

III. The availability of foods

The availability of invertebrates commonly taken by starlings at West Melton can be inferred from the birds diet. A coincident detailed study of pastoral invertebrates was made at Harewood, 15 km from West Melton, by Moeed (1970). As the areas appear similar in most respects, it is likely that the species composition and abundance of invertebrates are also

similar, so the main findings from Moeed's study are summarized here.

The Harewood insect fauna is divisible into a predominantly adult population throughout the warmer months of November to April and a larval one at other times. In summer, common are Coleoptera such as Costelytra zealandica and Aphodius howitti, dominants in October / November and January / February respectively, Hypharpax spp., Enneboeus sp., Coccinella spp., and various Elateridae and Curculionidae. Lepidoptera are also common, especially Crambus spp., Aletia sp., Persectania sp., Agrotis sp., Ariathisa comma, Wiseana spp. (in October and November) and Coleophora sp. (November to January), as well as Hemiptera such as Nysius huttoni, and Diptera, especially Sarcophaga milleri, Sarapogon sp. and Anabarrhynchus sp.

Common winter food species include the larvae of most summer forms. Exceptionally, Wiseana sp. larvae are abundant in surface layers from December to April but thereafter are found only at greater depths. Larval Diptera are common about the same time. Arachnids, particularly the families Lycosidae and Opilionidae, occur throughout the year but are most frequent in warmer seasons.

Sampling at West Melton revealed that earthworms are the commonest soil invertebrate throughout the year (see Coleman, 1968). Numbers are lowest in mid-November and apparently vary with changes in soil moisture. The availability of plant foods at West Melton, particularly cereal, is dependant on farming practices and also varies seasonally (see Ch. 6.3.II.).

IV. The foods of free-flying starlings

(a) Composition of the diet

The foods collected from free-flying starlings (assessed volumetrically) consisted of approximately 90% invertebrate and 10% plant remains, and included 75+ invertebrate species, 11+ seed species, some plant foliage, grit and one piece of meat (Table 18). Of these, fifteen animal species plus cereal, suckling clover (Trifolium dubium) and one unidentified larval group (flies) occurred in at least 20% of birds collected in one or more seasons, and were labelled dominant foods; they

Table 18. THE FOODS PRESENT IN THE GIZZARDS OF FREE FLYING STARLINGS

Food Species			Season							
			F M A		M J J		A S O		N D J	
ANIMAL FOODS			N+	%F+	N	%F	N	%F	N	%F
INSECTA										
ORTHOPTERA										
Gryllidae	Nemobius sp.		16	10.7	2	1.7				
Acrididae	Phaulacridium marginale		1	0.9						
DERMAPTERA										
Forficulidae	Forficula auricularia		8	1.8	6	1.7	16	10.7	5	3.0
HEMIPTERA										
Cicadellidae	Deltocephalus taedius		13	8.9	2	1.7			16	9.1
	D. coronifer				1	0.9				
Aphididae	Aulacorthum primulae		1	0.9						
Lygaeidae	Nysius huttoni		1454	61.6	444	38.8	713	51.8	2650	62.1
	Nysius sp.		58	8.0	4	0.9	4	1.8	2	1.5
Cydnidae	Philapodemus australis				77	0.9			1	1.5
	Cheesrocydnus nigrosignatus				64	0.9			5	1.5
Pentatomidae	Dictyotus caenosus		25	8.0	22	12.9	17	10.7	103	37.9
Reduviidae	Oncocephalus sp.		33	17.0	89	15.5	1	0.9	3	4.5
NEUROPTERA										
Hemerobiidae	gen. undet.				1	0.9				
LEPIDOPTERA										
Hepialidae	Wiseana	L.	25	7.1	158	29.5	124	25.9		
Coleophoridae	Coleophora sp.		62	10.7						
	" "	L.	101	13.4	211	17.2	270	25.0	234	31.8
Pyralidae	Witlesia sabulosella	L.	80	11.6	1728	56.6	1484	71.4	84	12.1
Crambidae	Crambus sp.		7	6.3			1	0.9	2	3.0
	" "	L.					1	0.9		
Pieridae	Pieris rapae				3	0.9				
	" "	L.	31	8.0						
Geometridae	"Xanthorrhoe" rosearia	L.	1	0.9					1	1.5
Noctuidae	Aristhisa comma		10	1.8						
	" "	L.	74	7.1	9	3.4	3	0.9		
	Agrotis ypsilon	L.	115	24.1	12	6.9	18	9.8	86	31.8
	Aletia temenaula	L.	13	4.5	8	3.4	2	0.9	20	7.6
	A. moderata	L.	1	0.9	6	3.4	4	2.7	6	1.5
	"Melanchra" mutans	L.			3	0.9			3	3.0
	Persectania aversa	L.	3	2.7						
	gen. undet.	L.	28	7.1	25	6.3	16	4.5	2	3.0
Hyponomeutidae	Plutella maculipennis				57	3.4				
	" "	L.	945	13.4	87	1.7			2	3.0
DIPTERA										
Asilidae	gen. undet.	L.					6	4.5		
	Necitamus sp.								10	4.5
Drosophilidae	Drosophila simulans		2	1.5						
	Scaptomiza graminum		1	0.9	2	0.9				
Muscidae	gen. undet.		9	4.5			1	0.9	2	1.5
	" "	L.	639	33.0	130	22.4	12	8.0	6	9.1
	Sarcophaga millari		56	21.4	8	6.0			94	12.1
Calliphoridae	Calliphora hortona		1	0.9						
	gen. undet.	L.	395	8.9	24	2.6			109	7.6
HYMENOPTERA										
Ichneumonidae	gen. undet.		4	3.6	75	13.8	12	8.9	1	1.5
Braconidae	Apanteles sp.		21	4.5						
Sphecidae	Tachytes sp.		5	1.8	1	0.9				
Pteromalidae	gen. undet.		1	0.9						
Formicidae	Chelaner antarcticus		1	0.9			5	0.9		
Sphecidae	Tachytes sp.		5	1.8	1	0.9				
Pteromalidae	gen. undet.		1	0.9						
Formicidae	Chelaner antarcticus		1	0.9			5	0.9		
COLEOPTERA										
Carabidae	Metaglymma monolifer		2	1.8	1	0.9	6	4.5	10	9.1
	Hypharpax antarcticus		30	9.8	19	5.2	6	3.6	12	9.9
	H. abstrusus		53	11.6	51	9.5	37	11.6	90	27.3
	Mecyclothorax rotundicollis		21	2.7	11	5.2	1	0.9		
Staphylinidae	Xantholinus sp.		28	17.0	10	8.6	44	18.8	20	18.2
	Oreophilus oculatus						6	5.4	3	1.5
Scarabacidae	Costelytra zealandica						8	1.8	283	40.9
	" "	L.	102	9.8	1073	37.1	559	26.8		
	Aphodius howitti		170	38.4						
	" "	L.					132	17.9	485	25.8
	Pyronota setosa						29	0.9		

Table 18. Cont.

Food Species			F M A		M J J		A S O		N D J	
ANIMAL FOODS										
INSECTA			N^+	$\%F^+$	N	%F	N	%F	N	%F
Elateridae	Lacon variabilis		183	58.0	259	68.1	124	58.9	119	60.6
	" "	L.	17	7.1	29	10.3	35	7.1	23	12.1
	Conoderus exsul				42	5.2	85	13.4	27	15.2
	" "	L.	2	1.8	1	0.9	26	16.1	3	4.5
Hydrophilidae	gen. undet.		4	0.9						
Cleridae	Necrobia ruficollis		3	0.9			1	0.9	2	3.0
Coccinellidae	Coccinella leonina		3	0.9	11	8.6	1	0.9	16	6.0
	" "	L.	3	1.8						
	C. undecimpunctata		1	0.9	6	5.2	3	2.7	3	3.0
	" "	L.	6	4.5						
Colydiidae	Pristoderus antarcticus		1	0.9						
	Coxelus instabilis		9	1.8			1	0.9		
Chrysomelidae	Atrichatus aeneicollis						1	0.9	14	3.0
Curculionidae	Gonipterus scutellatus		14	4.5			4	1.8	4	1.5
	Hyperodes bonariensis		429	78.6	497	58.6	726	77.7	453	65.2
	Irenimus aequalis		1905	92.9	1191	81.0	1351	82.1	1057	74.2
	Desiantha maculata		152	49.1	37	23.2	33	10.7	52	25.8
	Listroderes delaigue		26	11.6	49	14.7	9	5.4	90	18.2
	Otiorhynchus sulcatus		7	3.6	20	7.8	10	6.3	27	18.2
	Epitimetes griseatis				6	1.7	82	17.0	42	9.1
	Hylastes ater		2	0.9			2	1.8		
Apionidae	Apion ulicis						5	2.7	1	1.5
Tenebrionidae	Enneboeus sp.		1393	75.0	1295	84.5	349	53.6	126	47.0
	" "	L.	16	3.6						
Lathrididae	Melanophthalma gibbosa		5	3.6	1	0.9			1	1.5
ARACHNIDA										
ARANEIDA										
Lycosidae	gen. undet.		321	67.0	324	62.9	208	57.1	155	47.0
Salticidae	gen. undet.		2	1.8						
Agelanidae	gen. undet.		1	0.9	1	0.9				
Linyphiidae	Leptyphantes tenuis		2	1.8						
PHALANGIDA										
Phalangiidae	Phalangium opilio		9	6.3			1	0.9	6	6.1
CRUSTACEA										
ISOPODA										
	Porcellio scaber		10	3.6	12	7.8	1	0.9		
OLIGOCHAETA										
TERRICOLAE										
Lumbricidae	gen. undet.		8	17.0	52	45.7	80	62.5	1	12.1
MYRIAPODA										
CHILOPODA										
Geophilidae	gen. undet.		15	7.1	6	4.3	4	3.6		
Henicopidae	gen. undet.								1	1.5
OTHERS										
VERTEBRATE TISSUE "MEAT"			1	0.9						
PLANT FOODS										
* Gramineae	Triticum sp. / Hordeum sp.		48.4	58.0	20.5	25.8	41.7	8.0	34.5	16.7
Solanaceae	Solanum nigram		25	0.9						
	Hypochaeris sp.		3	0.9	3	2.6	2	0.9		
Compositaceae	Cirsium lanceolatum		4	0.9						
Caryophyllaceae	Spergula arvensis				2	0.9	2	1.8		
Polygonaceae	Polygonium persicaria				1	0.9	5	1.8		
Portulacaceae	Portulaca sp.				3	2.6	6	4.5		
Papilionaceae	Trifolium repens				2	0.9			5	6.1
	T. dubium				114	24.1	37	10.7		
	T. subterraneum		8	0.9						
Chenopodiaceae	Chenopodium album		3	2.7	14	3.4	1	0.9	9	6.1
* OTHER ITEMS										
Small stones					5.0	0.9			20.0	1.5
Grass / Plant material			40.0	2.7	40.0	3.0	6.0	6.3	5.0	1.5
SAMPLE SIZE			112		116		112		66	

Note - N^+, $\%F^+$ - Total numbers found and percent frequency respectively.
* 'Numbers' expressed as percentages.

included various life stages of two species of Hemiptera (plant bugs), two + species of Diptera (flies), four species of Lepidoptera (moths and butterflies), eight species of Coleoptera (beetles) and unidentified lycosid spiders and lumbricid earthworms. Other food species (approximately 57) were taken infrequently and were supplementary dietary components. Plant foliage and grit occurred infrequently and probably were ingested accidently.

Total counts of each food species present in gizzards were generally substantiated by percentage occurrence techniques (Table 18). A few medium to large foods were taken infrequently by many birds e.g. a cricket - Nemobius sp., an earwig - Forficula auricularia, a pentatomid bug - Dictyotus caenosus and such beetles as Lacon variabilis, Conoderus exsul and Xantholinus sp. Generally however, high percentage occurrence was indicative of items taken in large numbers, being especially true of smaller forms e.g. the "wheat bug" - Nysius huttoni (5261), larval pyralid moths - Witlesia sabulosella (3376), muscid fly larvae (787), lycosids (1008), a tenebrionid beetle - Enneboeus sp. (3163), a grass weevil - Irenimus aequalis (5504) and the Argentine stem weevil - Hyperodes bonariensis (2105).

The caloric energies (heats of combustion in Calories / g) of a range of foods commonly taken by adults and nestlings were similar (Table 19). However the caloric value of an average individual of each species and of its digestible components varied widely, the latter ranging from 0.513 Calories for Agrotis ypsilon larvae (the "Greasy cutworm") to 0.004 Calories for Nysius huttoni. Thus, resulting primarily from differences in biomass, one Agrotis larva was approximately equivalent in the energy of its digestible components to 2.4 earthworms, 5.6 Costelytra zealandica, 5.8 Neoitamus sp. (an asilid fly), 11.4 Conoderus larvae, 11.6 lycosids, 36.6 Irenimus aequalis and 128.3 Nysius huttoni.

The relative importance of these and closely related dominants, determined from caloric values extrapolated from the former, varied widely in the energy budget of free-flying birds (Table 20). Small forms like Nysius huttoni and Hyperodes bonariensis were taken frequently but contributed little towards the birds total sustenance. Conversely, larger forms, although taken in smaller numbers, often contributed greatly. Although

Table 19. CALORIC ESTIMATES OF A RANGE OF FOODS DOMINANT IN THE DIETS OF FREE-FLYING AND NESTLING STARLINGS

Food Species	Heat of Combustion of whole animal (Cal / g)	Mean dry Weight of species (g)	Mean Weight of chitin (g)	Mean Caloric Value* of digestible components (Cal)
Agrotis ypsilon L.	5.00	0.1080	0.0048	0.513
Nysius huttoni	5.30	0.0008	0.0001	0.004
Conoderus exsul L.	5.10	0.0109	0.0019	0.045
Costelytra zealandica	4.87	0.0216	0.0024	0.092
Irenimus aequalis	5.49	0.0032	0.0007	0.014
Neoitamus sp.	4.91	0.0235	0.0019	0.088
Lycosidae gen. undet.	5.37	0.0091	0.0006	0.046
Lumbricidae " "	5.36	0.0402	-+	0.216

Note - * The heat of combustion of an average individual minus the heat of combustion of the chitin present.

+ The chitin present in lumbricids was ignored, being within the limits of the equipment used.

the estimated caloric values of digestible tissues, and hence the total available energy for each species ingested, was slightly greater than that assimilated by starlings (see methods), from counts of foods taken it is apparent that the invertebrate groups contributing most towards the sampled birds well-being were larval Lepidoptera and adult and larval Coleoptera; Hemiptera and Diptera amongst common forms contributing little.

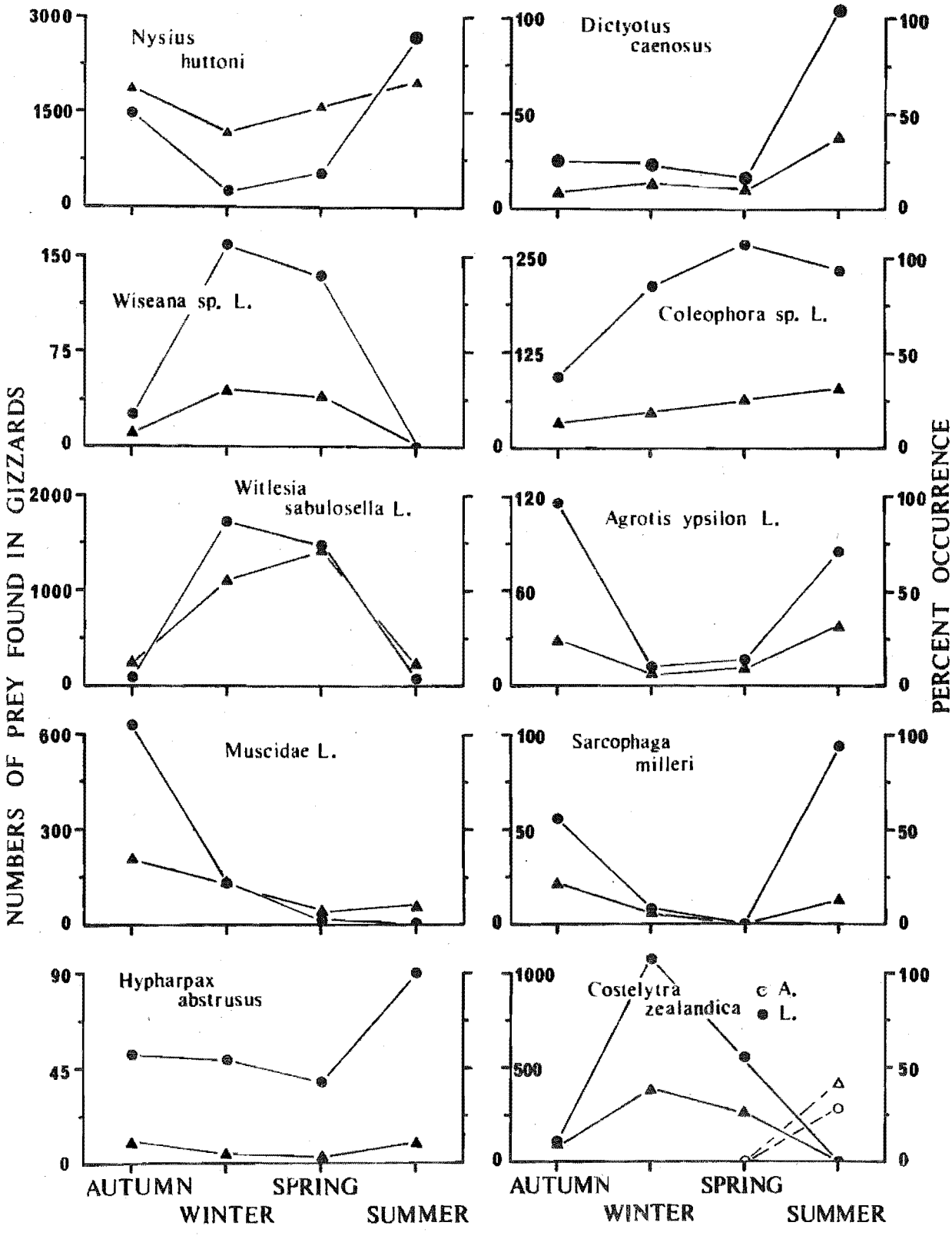
An accurate assessment of the caloric value of cereal grain ingested was more difficult to obtain. Grain averaged 10.4% by volume of gizzard contents throughout the year; the mean annual wet weight of the latter being 1.60 ± 0.068 g. Assuming that volumetric and gravimetric ratios of the animal and plant foods present were roughly equivalent, the weight of grain per bird and for all birds was 0.166 and 67.4 g respectively. Starlings ate a mixture of wheat and barley, but as they are of similar caloric value (approximately 3.5 Cal /g; Spector, 1956), no distinction was made. Thus, the value of grain present in all birds collected = 225 Calories and cereal appears to be a major element in the birds' energy budget.

(b) Variations in diet

(i) Seasonal variation

The dominant foods collected from starlings varied seasonally (Fig. 17). Species taken most commonly from birds shot during the dryer warmer months of November through to April included two Hemiptera - Nysius huttoni and Dictyotus caenosus, a fly - Sarcophaga milleri, three beetles - Aphodius howitti, Desiantha maculata and Hypharpax abstrusus and one Lepidopteran larva - Agrotis ypsilon. Conversely, species taken most frequently from birds shot during the moister, cooler months of May through to October included earthworms, two Lepidoptera larvae - Wiseana sp. and Witlesia sabulosella and a beetle - Costelytra zealandica. Other beetles like Enneboeus sp. and Lacon variabilis and larval muscid flies were taken most frequently from birds shot in autumn and winter, larval Coleophora sp. (Lepidoptera) from winter, spring and summer birds, and adult Costelytra zealandica and Coleophora sp. from summer and autumn ones respectively. Cereal remains were recovered throughout the year, but were taken erratically

A


Nysius huttoni
Dictyotus caenosus
Wiseana sp. L.
Coleophora sp. L.
Witlesia sabulosella L.
Agrotis ypsilon L.
Muscidae L.
Sarcophaga milleri
Hypharpax abstrusus
Costelytra zealandica
A.
L.
NUMBERS OF PREY FOUND IN GIZZARDS
PERCENT OCCURRENCE
AUTUMN
WINTER
SPRING
SUMMER

B

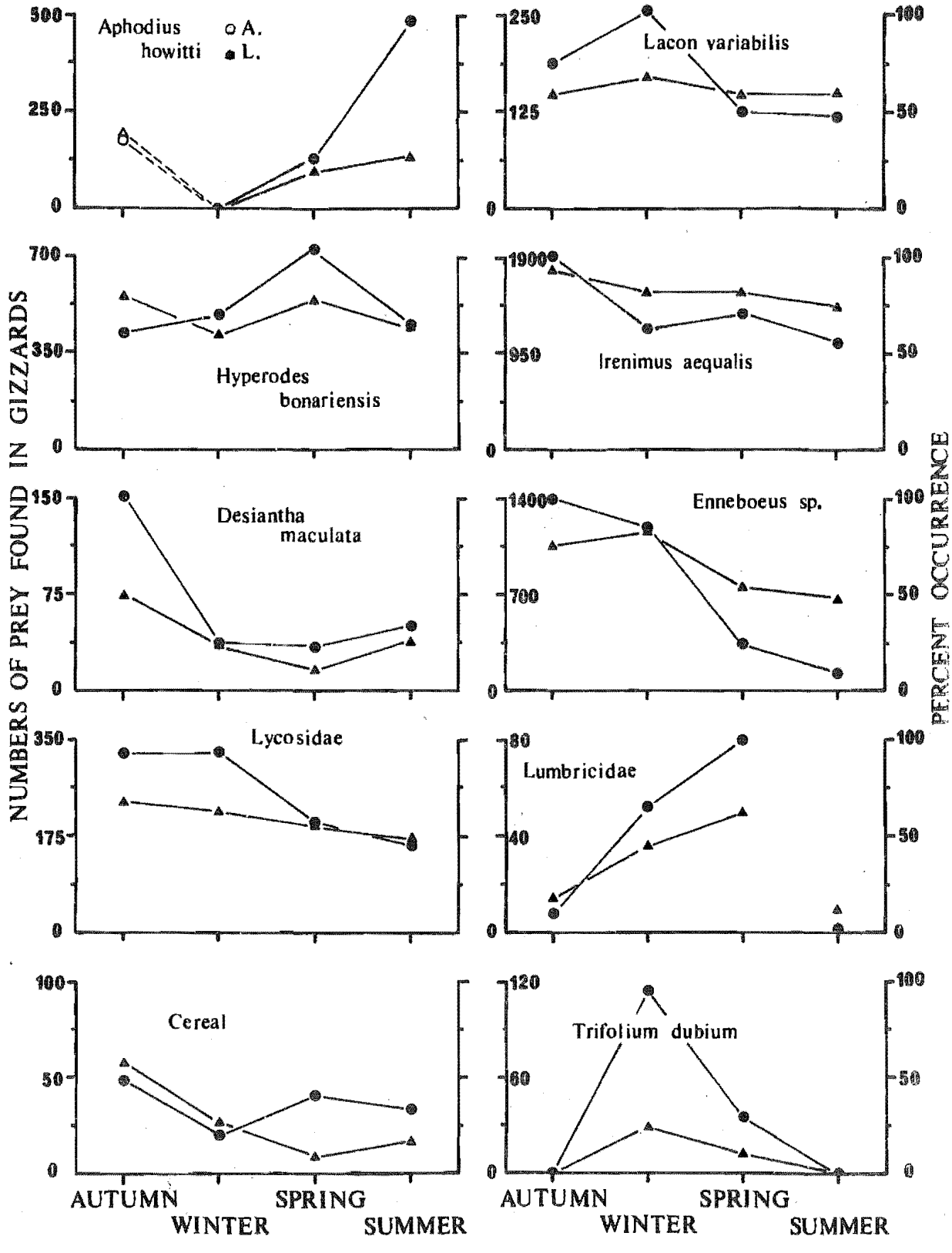

Aphodius howitti
o A.
• L.
Lacon variabilis
Hyperodes bonariensis
Irenimus aequalis
Desiantha maculata
Enneboeus sp.
Lycosidae
Lumbricidae
Cereal
Trifolium dubium
NUMBERS OF PREY FOUND IN GIZZARDS
PERCENT OCCURRENCE
AUTUMN
WINTER
SPRING
SUMMER
AUTUMN
WINTER
SPRING
SUMMER

Fig. 17, A - B.

Seasonal variation of foods dominant in the diet of free-flying starlings. Note that variations in total numbers of ingested prey (●) are similar to percentage occurrence analyses (▲) i.e. the percentage of birds taking each prey species.

Table 20. THE ENERGETICS OF THE DOMINANT ANIMAL FOODS OF FREE-FLYING STARLINGS

Food Species	Heat of combustion of entire animal (Cal /g)	Mean dry weight of species (g)	Mean weight of chitin of species (g)	Caloric value of digestible tissues (Cal)	No. of items taken from gizzards	Total energy of digestible tissue eaten (Cal)	Total energy ingested for each animal group (Cal)
Nysius huttoni	5.30	0.0008	0.0001	0.004	5261	21.04	
Dictyotus caenosus	-	0.0084	0.0011	0.039	167	6.51	27.55
Agrotis ypsilon L.	5.00	0.1080	0.0048	0.313	231	118.50	
Coleophora sp. L.	-	0.0005	-*	0.003	816	2.45	
Witlesia sabulosella L.	-	0.0123	0.0005	0.059	3376	199.18	
Wiseana sp. L.	-	0.1510	0.0061	0.725	307	222.57	542.79
Neoitamus sp.	4.91	0.0235	0.0019	0.088	10	0.8	
Sarcophaga milleri	-	0.0035	0.0005	0.025	158	3.95	4.75
Irenimus aequalis	5.49	0.0032	0.0007	0.014	5504	77.06	
Hyperodes bonariensis	-	0.0005	0.0001	0.002	2105	4.21	
Desiantha maculata	-	0.0040	0.0009	0.017	274	4.66	
Enneboeus sp.	-	0.0008	0.0002	0.003	3163	9.49	95.42
Costelytra zealandica	4.87	0.0216	0.0024	0.092	291	26.77	
Aphodius howitti	-	0.0200	0.0022	0.087	170	14.79	
Lacon variabilis	-	0.0163	0.0018	0.071	687	48.78	
Hypharpax abstrusus	-	0.0040	0.0005	0.017	231	3.93	105.71
Conoderus exsul L.	5.10	0.0109	0.0019	0.045	32	1.44	
Aphodius howitti L.	-	0.0220	0.0038	0.093	617	57.38	
Costelytra zealandica L.	-	0.0243	0.0042	0.103	1734	178.60	237.42
Lycosidae gen. undet.	5.37	0.0091	0.0006	0.046	1008	46.37	46.37
Lumbricidae gen. undet.	5.36	0.0402	-*	0.216	141	30.46	30.46

Note. The calculated heats of combustion of the first species in each group was considered representative of related forms. Likewise the percent chitin content determined for the first species was extrapolated to indented ones.

* The chitin present in lumbricids and Coleophora sp. was ignored, being within the limits of the equipment used.

in spring. Other dominants viz. Hyperodes bonariensis, Irenimus aequalis and lycosids were ubiquitous in all seasons.

The diversity of the starlings diet also varied seasonally (Table 18); numbers of species eaten departing significantly from a 1:1:1:1 ratio (X^2 = 10.15, 0.05 > p > 0.01). Many adult insects, particularly Hemiptera, Hymenoptera and Coleoptera were taken infrequently and only during warmer months; their immature stages occurring in other seasons probably being more secretive and / or broken down more readily in gizzards.

(ii) Variations with feeding site

Many of the starlings foods were wide-ranging in habit but others were specific to crop or field type (Table 21). Birds collected from pasture, turnip or cereal stubble fields on average contained many Nysius huttoni, Enneboeus sp., Hyperodes bonariensis, Irenimus aequalis and lycosids. Conversely, common forms specific to field types included Witlesia sabulosella, adult Costelytra zealandica and larval Aphodius howitti from pasture, Plutella maculipennis and muscid fly larvae from turnips, cereal grain from cereal stubble and larval Wiseana sp., Costelytra zealandica and lumbricids from cultivated fields; the latter taken during tilling. Five birds were collected on irrigated summer pasture and each contained several lumbricids; a food rarely taken in that season.

(iii) Variations with age

The dominant foods of adult and recently fledged (within one month) starlings were identical. Also, diet diversity was independent of age; all (20) birds of either age group collected on pasture in December and February taking a similar range of foods (X^2 = 0.024, 0.9 > p > 0.5). Young starlings apparently recognise food species early in life and do not appear to be more exploratory in their feeding than older birds c.f. young wood pigeons - Columba palumbus which eat a wider range of foods than their parents (Murton, Isaacson and Westwood, 1971).

The number of items present in the gizzards of birds in the above sample were on average greater in adults (123.6) than juveniles (84.6); differences approaching significance (F_s = 2.09, 0.1 > p > 0.05; F_s (0.05) = 2.12). Compared with recently fledged birds, it appears that adults feed more intensively and / or successfully, (also shown for wood pigeons, Murton, Isaacson and Westwood, op.cit.). This appears to

conflict with a proven independence of age with the wet weight of gizzard contents (Ch. 8.3); the lack of significance in the latter possibly being due to high sample variance.

V. The food brought to the nest

(a) Composition of the diet

The foods collected from nestlings were mostly invertebrates with arthropods predominant (50+ spp.), although lumbricids (spp.), arachnids (2 spp.), myriapods (1 sp.) and a gastropod mollusc were also taken (Table 22). Cherries were occasionally eaten. Apart from an isopod crustacean, all the Arthropoda eaten were insects with Hemiptera, Lepidoptera, Diptera and Coleoptera predominant; the last three commonly taken as adults and larvae. Dominant food species (those collected in two or more years in more than 10% of all food samples) were few in number, and in order of percentage occurrence included Agrotis ypsilon larva, lycosid spiders (spp.), Costelytra zealandica, Nysius huttoni, earthworms (spp.), Irenimus aequalis, Conoderus exsul larva, and Neoitamus sp. Species recorded less frequently, but taken by 10% or more of birds in one of the three years of study, included Dictyotus caenosus, Agrotis ypsilon, Muscid flies (spp.), Lacon variabilis, Coccinella undecimpunctata, Phalangium opilio - an opilione, and, Metaglymma monolifer, Hypharpax antarcticus and H. abstrusus - all carabid beetles.

With few exceptions, total counts of individuals of food species collected from nestlings gave results similar to those obtained by the use of percentage occurrence techniques (Table 22). Individuals taken in greatest number, in order, included Nysius huttoni (800), Costelytra zealandica (385), Agrotis ypsilon larva (268), Phalangium opilio (258), lycosid spiders (255), Hypharpax antarcticus (193), H. abstrusus (188), Coleophora sp. (161), Irenimus aequalis (124) and Conoderus exsul larva (113).

The caloric value of the digestible components of dominant foods and the numbers ingested of each varied widely (Table 23), as did their relative importance in the nestlings' energy budget. Thus, of the energy content of dominant foods present in the food samples collected, 61.6% was derived from Agrotis larvae, with Costelytra zealandica (15.8%), lumbricids

Table 22. THE FOODS OF NESTLING STARLINGS

Food Species		1969		1970		1971	
INSECTA		N*	%**	N	%	N	%
ORTHOPTERA							
Acrididae - Phaulacridium marginale		1	0.5				
Stenopelmatidae - Hemiandrus similis		1	0.5	1	1.1		
DERMAPTERA							
Forficulidae - Forficula auricularia		3	1.0	1	1.1	10	4.4
HEMIPTERA							
Cicadidae - Melampsalta sp.		6	2.6	1	1.1	7	6.6
Lygaeidae - Nysius huttoni		609	33.8	20	7.9	171	28.6
- Nysius sp.		3	1.5				
Pentatomidae - Dictyotus caenosus		7	3.6	4	2.2	24	15.4
Cixiidae - Oliarus oppositus		1	0.5				
LEPIDOPTERA							
Hepialidae - Wiseana sp.		28	2.6				
" "	L.	10	3.1	1	1.1		
Oecophoridae - Atomotricha sp.		2	0.5				
Coleophoridae - Coleophora sp.		25	2.6	8	1.1	128	4.4
" "	L.	2	0.5				
Pyralidae - Witlesia sabulosella		18	5.6	16	3.4		
" "	L.					10	5.5
Ephestia elutella				1	1.1		
Crambidae - Crambus sp.	L.	16	5.6	2	1.1	4	2.2
Tineoidae - Tineola biselliella	L.			2	1.1		
Pieridae - Pieris rapae		1	0.5				
Noctuidae - Agrotis ypsilon		43	15.4				
" "	L.	83	32.8	21	15.7	164	61.5
- Ariathisa comma	L.	12	4.1				
- Aletia moderata		3	1.5				
" "	L.	6	2.6				
- A. temenaula	L.			1	1.1		
- "Melanchra" mutans	L.	2	1.0				
- Persectania aversa		4	1.5				
" "	L.	10	2.6			14	8.8
Hyponomeutidae - Plutella sp.						2	2.2
DIPTERA							
Therevidae - Anabarrynchus sp.		2	0.5				
" "	L.	2	1.0				
Asilidae - Saropogon sp.		11	3.1			1	1.1
Neoitamus sp.		46	12.8	32	20.2	15	8.8
" "	L.	1	0.5				
Syrphidae - Melanostoma fasciatum		1	0.5	2	2.2		
Muscidae - spp.		35	6.2	4	4.5	23	13.2
"	L.			10	3.4	36	3.3
Calliphoridae - Calliphora sp.				1	1.1		
Calliphora laemica	L.	15	0.5	9	4.5		
Calliphoridae	L.	5	2.6				

Table 22. Cont.

Food Species		1969		1970		1971	
INSECTA		N*	%**	N	%	N	%
HYMENOPTERA							
Ichneumonidae - Pterocormus sp.		3	1.0			1	1.1
Pompilidae - Crytocheilus sp.		1	0.5				
COLEOPTERA							
Carabidae - Megadromus sp.						1	1.1
Metaglymma monolifer		11	4.6			44	25.3
Hypharpax antarcticus		13	5.6	5	5.6	175	22.0
H. abstrusus		32	6.7	5	4.5	151	28.6
Staphylinidae - Xantholinus sp.	L.	1	0.5				
- Creophilus oculatus						1	1.1
Scarabaeidae - Costelytra zealandica		292	42.1	15	14.6	82	29.7
Aphodius howitti		15	2.1			11	4.4
Pyronota setosa		4	2.1				
Elateridae - Lacon variabilis		13	5.1	3	3.4	79	28.6
" "	L.			1	1.1		
Conoderus exsul		7	3.6			15	12.1
" "	L.	28	12.3			85	35.2
Dermestidae - Dermestes maculatus		3	1.0				
Cleridae - Necrobia ruficollis		4	1.5				
Coccinellidae - Coccinella undecimpunctata		22	4.6			19	11.0
Chrysomelidae - Paropsis charybdis		1	0.5				
Atrichatus aeneicollis				1	1.1		
Curculionidae - Desiantha maculata		2	1.0				
Irenimus aequalis		38	12.8	20	10.1	66	22.0
Hyperodes bonariensis		9	2.1			2	1.1
Listroderes delaigue		16	1.5				
Tenebrionidae - Mimopeus sp.		2	1.0			1	1.1
Enneboeus sp.						6	4.4
ARACHNIDA							
ARANEIDA							
Lycosidae spp.		88	24.1	31	29.2	136	41.8
PHALANGIDA							
Phalangiidae - Phalangium opilio		236	19.5	14	5.6	8	5.5
CRUSTACEA							
ISOPODA - Porcellio scaber		21	5.1	1	1.1	26	6.6
MYRIAPODA							
CHILOPODA							
Gonibregmatidae - spp.		2	0.5				
ANNELIDA							
OLIGOCHAETA							
Lumbricidae spp.		31	15.4	37	33.7	30	17.6
MOLLUSCA							
GASTEROPODA - Physia sp.						1	1.1
PLANT FOODS							
ROSACEAE - Prunus avium		30	0.5				

Note: N* = Number of individuals collected in total sample
%** = Percent occurrence - see text
Underlined values show foods "dominant" in any season

Table 23. / THE ENERGETICS OF THE DOMINANT FOODS OF NESTLINGS

Food Species	+Mean Caloric value of digestible components (Cal)	Number of animals taken from nestlings	Total energy of digestible tissues taken (Cal)
Agrotis ypsilon L.	0.513	268	137.40
Nysius huttoni	0.004	800	2.88
Conoderus exsul L.	0.045	113	5.06
Costelytra zealandica	0.092	385	35.23
Irenimus aequalis	0.014	124	1.69
Neoitamus sp.	0.088	93	8.16
Lycosidae gen. undet.	0.046	255	11.60
Lumbricidae " "	0.216	98	21.19

Note - + - Values determined in Table 19

(9.5%) and lycosids (5.2%) of lesser importance. Other species such as Neoitamus sp. (3.7%), Conoderus exsul (2.3%), Nysius huttoni (1.3%), and Irenimus aequalis (0.76%) were taken frequently by many individuals (Table 22), but individually were of little consequence.

(b) Variations in the foods taken

The dominant food species recorded from nestlings in 1969 were generally also dominants in 1970 and 1971 (Table 22). In addition, a further five beetle species were commonly recorded in 1971 viz. adult Hypharpax antarcticus, H. abstrusus, Lacon variabilis, Coccinella undecimpunctata and Metaglymma monolifer. These were recovered more frequently apparently because of the different methods of investigation used (gizzard analysis), which biased diet patterns towards the harder species present (see Ch. 7.1).

The variety of food species collected from nestlings in 1969 (48 + spp.) was greater than in 1970 (28 + spp.) or in 1971 (31 + spp.). However, more than half of all collections were taken in 1969, when the adults of numerous beetle, moth and fly species were recorded casually.

The percentage occurrence and total counts of individuals of dominant food species co-varied as the breeding season progressed (Fig. 18). Species collected most frequently from later-hatched nestlings included Nysius huttoni, Phalangium opilio and lumbricids. Conversely, Neoitamus sp. and Agrotis ypsilon larva were taken most frequently from earlier broods, with Neoitamus sp. absent from December samples. Other dominants failed to show consistent seasonal trends.

The diet of nestlings in 1969 became more diverse as the breeding season progressed, with the periods November 3 - 17 (N = 36), 18 - 25 (N = 39) and after December 4 (N = 33) averaging 0.70, 0.79 and 1.00 new food species per sample respectively. Samples collected between November 26 and December 3 (N = 87) were too numerous for comparison. The diet of nestlings in late broods was diversified by the December maturation and occurrence of many adult beetle and fly species.

The numerical frequency of some food species taken by nestlings varied with nestling age (Table 24). Birds aged 0 - 5 days received fewer individuals of "hard" food species such as adult Coleoptera, especially Costelytra zealandica,

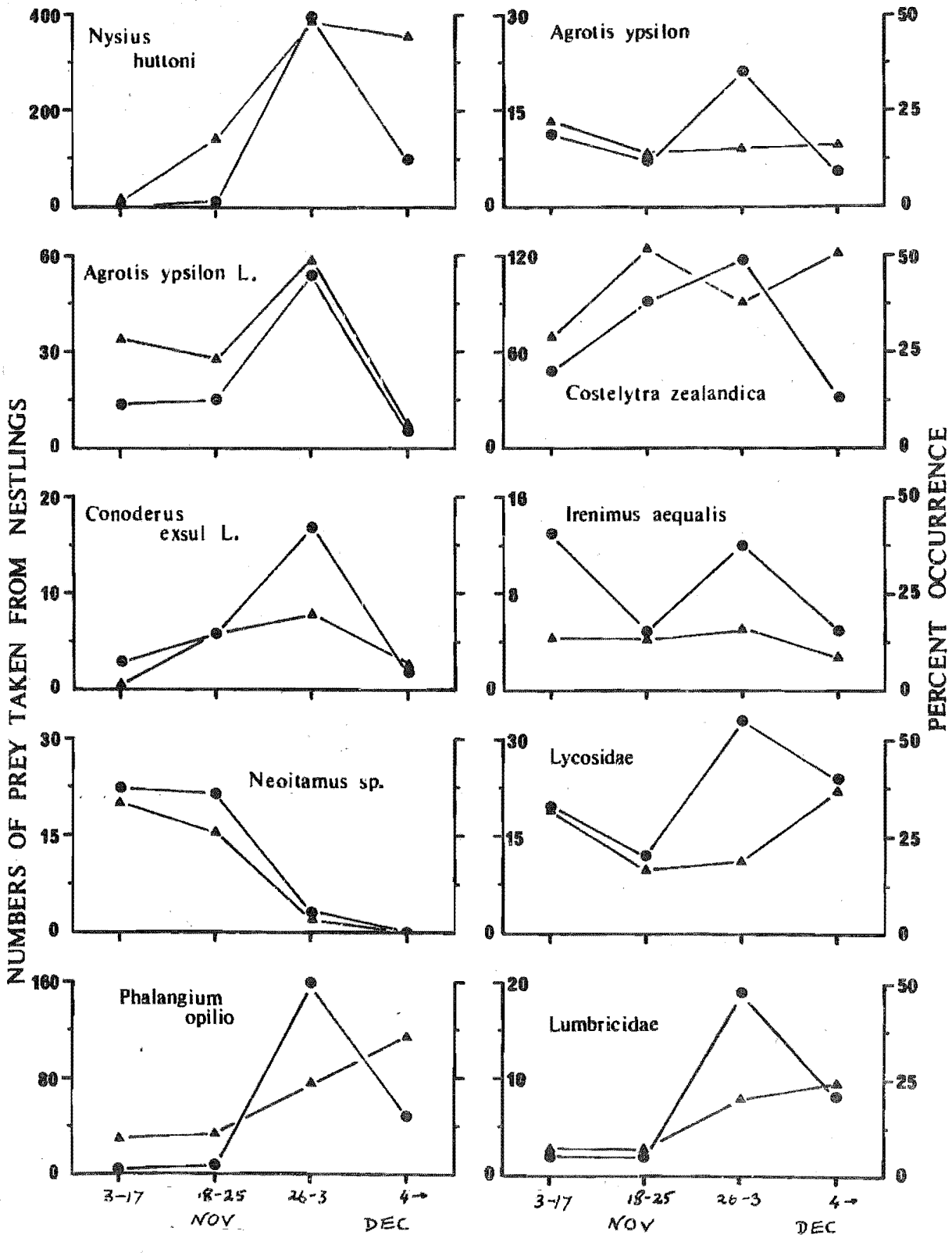

Nysius huttoni
Agrotis ypsilon
Agrotis ypsilon L.
Costelytra zealandica
Conoderus exsul L.
Irenimus aequalis
Neoitamus sp.
Lycosidae
Phalangium opilio
Lumbricidae
NUMBERS OF PREY TAKEN FROM NESTLINGS
PERCENT OCCURRENCE
3-17
18-25
26-3
4→
NOV
DEC

Fig. 18

Seasonal variation in total numbers (● - ●) and percent occurrence (▲ - ▲) of foods dominant in the diet of nestling starlings.

Table 24. VARIATION IN THE DIETARY COMPONENTS OF NESTLING STARLINGS IN RELATION TO THEIR AGE

Foods Taken		Age of Nestlings (Days)					
		0 - 5		6 - 11		12 +	
		N	%F	N	%F	N	%F
Arachnida							
Lycosidae		59	11.0	38	3.8	22	4.1
Opilionidae		35	6.5	72	7.2	143	26.7
Lumbricidae		17	3.2	40	4.0	11	2.1
Insecta							
Hemiptera		177	32.9	266	26.5	107	20.0
Coleoptera	A.*	60	11.2	320	31.8	148	27.6
	L.**	7	1.3	16	1.6	5	0.9
Lepidoptera	A.	64	11.9	71	7.1	12	2.2
	L.	57	10.6	68	6.8	44	8.2
Diptera	A.	45	8.4	83	8.3	14	2.6
	L.	5	0.9	21	2.1	16	3.0
Others		12	2.2	10	1.0	14	2.6
N		538		1005		536	

Note: Table includes data from gullet samples collected from 287 nestlings in 1969 and 1970.

A.* = Adult, L.** = Larva

than their older conspecifics. Conversely, softer foods including lycosid spiders, larval and adult Lepidoptera, and Hemiptera occurred most commonly in samples taken from the youngest nestlings; opiliones being the anomaly in this pattern.

(c) The size of meals

Newly-hatched nestlings received small meals, often consisting only of single individuals of soft-bodied invertebrates such as small arachnids or moth larvae. Older nestlings had larger and more varied meals e.g. those of a brood of four averaged 0.06 $\pm$ 0.005 g (N = 16) and 0.07 $\pm$ 0.008 g (N = 24) dry weight, when aged four and eight days respectively (differences not significant). Individuals at both ages received a similar number of food items per meal (2.1 and 2.0 for 4 and 8 day chicks respectively), but the younger birds received different and slightly smaller prey species.

Older nestlings received prey ranging in size from large noctuid moth larvae 30 mm long (Mean = 0.11 g dry weight; N = 20) to nymphal aphidid bugs 2 mm long (Mean = 0.001 g dry weight; N = 50); adults themselves ate prey within that size range. Meals consisted of one to ten items, depending on the size of the component species. A single lumbricid or noctuid larva often constituted a meal, but small bugs, weevils or colonial sarcophagid fly larvae were taken several at a time.

(d) Feeding frequencies

The parents of four broods were observed for a total of 17 hr and 20 min. On average they fed their nestlings every 6.5 min, with means of from 3.7 to 9.1 min (Table 25). Neither brood age nor size appeared to influence the frequency of visits but the rate was consistently highest in late afternoon and lowest about midday. Overseas workers recorded similar diurnal feeding patterns i.e. Szijj (1956), Kessel (1957).

The number of nestlings fed at each visit varied with the age of the brood. When four days old, two out of four nestlings in a brood of four were fed on 12 of 16 visits, and one on each of the other four occasions. Four days later this pattern had reversed; only one nestling received food on 24 of 26 visits, and two nestlings on the remaining visits. When

Table 25. THE FREQUENCY OF PARENTAL FEEDING VISITS TO BROODS

Date	Box No.	Nestling Age (days)	Brood Size	Time of observation	Total time (min)	No. of Visits	Visit frequency
12.11.69	Th.39	9	3	1320-1500	100	12	1/8.3
21.11.69	"	18	2	1310-1355	45	5	1/9.0
21.11.69	Th.38	20	2	1215-1355	100	11	1/9.1
1.11.70	So.14	7	3	1540-1705	85	19	1/4.5
6.11.70	"	12	3	1445-1625	100	27	1/3.7
30.11.70	Th.40	4	4	1000-1400	240	33	1/7.3
4.12.70	"	8	4	0920-1530	370	52	1/7.1

parents arrived simultaneously, the nestling which begged most vigorously received the most food.

(e) Feeding rates as a measure of food intake

In Holland, starlings with broods foraged daily from sunrise to sunset (Kluijver, 1933) and this was true for Canterbury birds also. In Canterbury, in mid-November there were 14 hr and 35 min of foraging time available each day. Adults averaged 134.6 brood visits daily or, if averaged over the nestling period of 22 days, 48.1 meals / day / nestling for a brood of three (allowing for the feeding of two nestlings per parental visit during the first four days) c.f. 83 meals per day averaged over the nestling period of a brood of four, Kluijver (op.cit.), cited by Lack (1948). As quantitative observations in Canterbury were confined to the mid-morning period and later, thus excluding the early morning period when feeding was probably most rapid (Kluijver, op.cit.; Szijj, 1956), the mean feeding frequency obtained was probably low. However, it seems unlikely that feeding rates in Canterbury would be as high as Kluijver's data for Dutch starlings suggest.

If nestlings in broods of three and four receive meals of similar size, at eight days of age each would ingest daily 3.4 g dry weight of food (= 48.1 x 0.07). Roughly 10% of the food ingested is non-digestible chitin (Table 19) and a further 20% of that remaining is lost as metabolic wastes (see methods). Hence, approximately 2.46 g of the daily intake is metabolizable. The daily energy intake of each nestling is 2.46 x 5.2 Calories or approximately 12.82 Cal / day (5.2 Cals being the approximate caloric value of the dominant foods eaten; see Table 20). However, it must be stressed that this figure is at best an approximation and needs further study.

4. CONCLUSIONS

I. Feeding activities

Starling flocks differ seasonally in size and behaviour. Throughout the year, but especially at breeding, birds generally occur in loosely integrated, slow-moving flocks of 5 to 30 which are often closely associated with stock. In the non-

breeding period, large co-ordinated flocks of up to 500 birds occur. Members of the latter probably have an advantage over those in looser aggregations. They appear to exploit foods more efficiently through the "beating" of neighbours (also recorded by Rand, 1954), often taking foods immediately behind adjacent birds, while the frequent co-ordinated aerial flocking following alarms is a method of predator detection common to many bird species (Hinde, 1961).

The feeding actions of starlings are affected largely by the nature and habit of their food. Subterranean forms are obtained by "deep probing" or "following the plough"; sward dwellers by "pecking", "surface probing" or "arboreal pecking"; those in dung by "dung turning", and highly mobile forms by "jumping" or "pouncing".

Feeding ranges vary seasonally. During breeding, parent starlings forage on pasture within 500 m of their nest sites c.f. ranges of up to 1500 m for Starlings in Holland (Kluijver, 1938), 1600 m in Scotland (Anderson, 1961) and 2000 m in Finland (Tenovou and Lemmetyinen, 1970), differences resulting from the selection of feeding sites. At other times birds forage from communal roosts, although adults often still feed about old nest sites. Even so, ranges of up to 4 km appear maximal for all age groups.

II. Selection of feeding sites and food

Starlings frequent open country and rarely feed in wooded areas (Kluijver, 1938). In the former, they show seasonal preferences for particular field types as feeding sites, apparently due to phenological differences in pasture and crop maturity and in associated insect populations e.g. in Czechoslovakia starlings select fields of lucerne, marshlands and "green crops" in spring, grass in summer, and cultivated fields in autumn and winter (Szijj, 1956); in Scotland, cereal stubbles in autumn and generally pasture in winter (Dunnet, 1956) although, like birds in Utah, U.S.A. (Bailey, 1966), Scottish starlings seek artificial foods during adverse winter weather.

In Canterbury, starlings also vary their feeding sites seasonally. In spring, summer and autumn birds select pasture fields, especially well-grazed grass. Supplementary foods are obtained in spring from fields being tilled, and in summer and

autumn from cereal stubbles. In winter, starlings select fields of turnips and other fodder crops and also occasionally take cereal from stock feed lots; the latter, however, are available for stock, and therefore starlings, only after unusually dry autumns. Starlings generally avoid emergent, rank or mature cereal, peas, potatoes, emergent turnips and lucerne, but the use or avoidance of all fields is markedly affected by stock; in particular, birds in small flocks select fields with stock and use them as "beaters" c.f. starlings in Scotland which are infrequently associated with stock (Dunnet, 1955). Overall, the bulk of Canterbury starlings feed on pasture. Selections favouring less frequent field types generally involve only a small percentage of all birds censused e.g. 5% follow the plough in spring (Fig. 16) and 2% feed amongst rank cereal in winter (Fig. 15). Conversely, winter pasture though selected against, still suports approximately 36% of all birds observed.

Starlings have frequently been termed "generalistic" feeders as their diet often reflects the natural abundance of their foods e.g. Kluijver (1933), Dunnet (1955), Korol'kova (1963), Davis (1967), Gromadski (1969). However, recent studies have shown that many bird species feed selectively through searching images (see Tinbergen, 1960; Croze, 1970; Royama, 1970) utilizing such factors as prey palatability (e.g. tits-Parus spp., Tinbergen, 1960), nutritive value (e.g. Icelandic ptarmigan - Lagopus mutus, Gardasson and Moss, 1970), abundance (e.g. Parus spp. - Tinbergen, op.cit.; Royama, op.cit.) and prey size and hardness (Tinbergen, op.cit.). Further, selectivity may be periodic, tits and goldcrests (Regulus regulus) being strongly selective during periods of great food abundance (Gibb, 1954, 1960) and less fastidious at other times.

Canterbury starlings also show distinct dietary preferences. During the nestling period, parents select food of a size and hardness suitable for nestlings and apparently ignore common, large, "hard" bodied beetles and similar foods. Starlings in North America (Kalmbach and Gabrielson, 1921), blackbirds Turdus merula in Germany (Korodi-Gal, 1967) great tits Parus major in Britain (Royama, op.cit.) and Arctic terns Sterna paradisaea (Hawksley, 1957) show similar changes of prey

selection. Preferences of Canterbury birds appear to extend outside of breeding; caged adults and first year birds preferring soft-bodied larvae and spiders to harder forms.

The diet of juvenile and adult starlings is similar in content and diversity, and preferences are apparently established in the first post-fledging month. However, adults feed more successfully, presumably due to experience (also shown for wood pigeons, Murton, Isaacson and Westwood, 1971, and cattle egrets - Ardeola ibis, Siegfried, 1972). Juvenile wood pigeons spend considerable periods watching and learning from the feeding of older birds, but young starlings acquire such knowledge more rapidly. Throughout most of the year overall dietary patterns agree closely with the natural abundance of food species and starlings appear to follow Lack's (1970) tenet viz. that animals select food not only in relation to their physiological needs but also with regard to the ease with which foods are captured.

III. Diet of free-flying and nestling starlings

The diet of free-flying rural starlings has been documented many times but results have often been non-quantitative and / or anecdotal. Basic dietary patterns established overseas have usually been similar to one another although the relative importance of animal and plant groups varies according to local species abundance, land use and methods of analysis. Thus, studies made in viticultural regions of Australia (Thomas, 1957, a - e) or Hungary (Szijj, 1956) or in cherry growing areas in New England, U.S.A. (Kalmbach and Gabrielson, 1921; Kalmbach, 1922), Czechoslovakia (Havlin and Folk, 1965), Hungary (Szijj, op.cit.) and Germany (Haberkorn, 1962) show expected preponderances of grapes (Vitis sp.) and cherries respectively, while others made in pastoral communities reveal a dominance of invertebrates and a lack of plant foods e.g. Pfabe and Szypula-Gador (1964), Russel (1971), Lobb and Wood (1971).

The starlings apparent granivorous tendencies are enigmatic; Kalmbach and Gabrielson (op.cit.), Szijj (op.cit.) and Havlin and Folk (op.cit.) report that grain is taken in small quantities and only when major foods are in short supply, while Collinge (1924-27), Dunnet (1956) and Bailey (1966) consider cereal to be a staple food. However, it is likely

that grain is not as important as some authors believe; foods break down differentially in the starlings gizzard and cereal grains are retained longer than animal remains (see Ch. 7.3).

Animal foods are without exception dominated by the Insecta. Of these, Coleoptera appear to constitute the largest fraction taken in most areas, with the families Curculionidae, Carabidae and Scarabaeidae also important e.g. Kalmbach and Gabrielson (1921), Szijj (1956), Havlin and Folk (1965), Shadowen (1969), Gromadski (1969) and Russel (1971). Other major food groups include the Orthoptera - Kalmbach and Gabrielson (op.cit.), Korol'kova (1963), Russel (op.cit.), Lepidoptera - Lindsey (1939) and Diptera - Gromadski (op.cit.), Dunnet (1956). Miscellaneous foods are taken in much smaller numbers but may become important when major foods are scarce.

Starlings in New Zealand eat similar foods to overseas birds. Early workers emphasised the apparent ability of the species to control invertebrate pests, especially Lepidoptera larvae and Coleoptera (Bathgate, 1897) and also Orthoptera and the ectoparasites of stock (Thompson, 1922). Thompson also listed as common foods cultivated fruits such as pears (Pyrus sp.), plums, peaches (both Prunus spp.) and cherries. More recently, Dawson and Bull (1970) listed a similar array of fruits commonly eaten by starlings while Caithness (1968), Moeed (1970) and Lobb and Wood (1971) concurred as to the pastural invertebrates taken; the latter authors working close by my study area. At Winchmore (Lobb and Wood, op.cit.) and Harewood (Moeed, op. cit.), starlings feed primarily on Coleoptera, especially Curculionidae (weevils - largely Hyperodes and Irenimus spp.), Scarabaeidae (predominantly Costelytra zealandica) and members of the Elateridae. Other major foods include Hemiptera, especially Nysius huttoni, and Lepidoptera, particularly Agrotis ypsilon, Wiseana spp. and Coleophora spp. Most staple foods are taken throughout much of the year, with only Costelytra zealandica distinctly seasonal. Miscellaneous foods listed only for Harewood, included members of most remaining insect orders as well as earthworms, arachnids and cereal.

The diet of independent West Melton birds is similar, often to species level, to that of neighbouring populations. Animal foods predominate (approximately 90% by volume); the remainder largely being cereal but including a wide range of

infrequently eaten clover (Trifolium spp.) and weed seeds. Small seeds may be eaten accidently; they escape digestion and presumably are disseminated still viable throughout the study area (also recorded by Havlin and Folk, 1965). Fruits are rarely taken.

Caloric evaluations of the diets of Canterbury birds alter the numeric level of importance of some major foods. Lepidoptera, especially larval forms such as Wiseana spp., Coleophora spp., Witlesia sabulosella and Agrotis ypsilon dominate. Coleoptera are next in importance consisting primarily of the Curculionidae especially Hyperodes bonariensis and Irenimus aequalis, followed by highly seasonal scarabaeids - especially Costelytra zealandica and Aphodius howitti, and the more universal carabids - Metaglymma monolifer and Hypharpax spp. and Elaterids - Lacon variabilis and Conoderus exsul. Hemiptera particularly Nysius huttoni are taken in large numbers throughout the year, but like less commonly taken insect orders such as Diptera, Orthoptera, Hymenoptera and Dermaptera, are apparently of little caloric consequence. Arachnids, lumbricids and cereal are important minor dietary elements.

Dietary patterns of West Melton birds vary seasonally in content and diversity, and generally follow trends in the abundance of soil invertebrates established at Harewood (Moeed, 1970), with adult insects dominant in the warmer dryer months and larval forms, arachnids and earthworms relatively more common at other times. Thus, the natural abundance of common forms was probably similar in both areas; one notable exception to this concurrence being Agrotis ypsilon which was abundant at Harewood only in winter but a major spring food at West Melton - differences which may arise from Moeed's (op.cit.) sampling methods, as he presents data for Lepidoptera "with some reservation".

Diet varied with feeding sites. Although some foods were apparently ubiquitous and others specific to particular field types, still others were available only during specific farming operations. Hence, pastural pest species particularly scarabaeid beetles (Costelytra zealandica and Aphodius howitti) were peculiar to pasture, although their larvae and that of pasture-inhabiting Lepidoptera (particularly Wiseana spp.)

and earthworms were taken frequently during tilling operations when otherwise unavailable. Likewise irrigated fields served as a source of "unseasonal foods". Cereal grain was taken primarily from stubble fields and secondarily from stooked oats and winter feed-lots.

Nestlings at West Melton eat similar foods to concomitant free-flying birds (see Tables 18 & 22) i.e. predominantly Lepidoptera larvae, Coleoptera, Hemiptera, Diptera and Lumbricidae, although very young nestlings are fed a more restricted diet c.f. Korol'kova (1963), Gromadski (1969). Nestling diets are also similar to, but broader than, those of nestlings in other countries e.g. in Scotland - Diptera larvae 80%, earthworms 16% (Dunnet, 1955); in the U.S.S.R. - Lepidopteran larvae 82% (Korol'kova, 1963); in Poland - Coleoptera 53%, Diptera 23%, earthworms 15% (Gromadski, 1969).

Caloric evaluations of Canterbury nestling diets also follow patterns established for local adults i.e. small forms ingested in large numbers such as Hemiptera and Curculionidae contribute minimally towards the nestlings sustenance, while common larger forms, especially Lepidopteran larvae and scarabaeid beetles, form the bulk of the ingested energy.

Overall, nestling foods are similar each year but the abundance of dominants varies seasonally; diets become more diverse with the December emergence of adult Coleoptera and Diptera and the accompanying loss of some larval forms (also recorded by Gromadski, 1969).

Meal size varies with nestling age but is apparently maximal when nestlings are four to five days old. Meal sizes in Holland increase until 12 to 15 days after hatching (Kluijver, 1933), but birds in Scotland (Dunnet, 1955) show trends similar to Canterbury starlings.

The numbers of meals received daily by nestlings depends on brood age and size. Like broods in Holland (Kluijver, op.cit.) only one nestling in all but the youngest of Canterbury broods is fed during each parental visit, with those in large broods being fed less frequently. Nestlings in average sized broods receive approximately 48 meals per day throughout their nestling period; a minimal daily energy intake of 13 Calories.

CHAPTER 7

BREAKDOWN RATES OF INGESTED FOODS

1. INTRODUCTION

Investigations of the diet of birds have generally been based on numeric, volumetric or gravimetric analyses of food remains in the stomach e.g. 95% of 125 studies on waterfowl foods published between 1901 and 1965 were based wholly or in part on food remains in this organ (Bartonek, 1968; cited by Swanson and Bartonek, 1970). However, Van Koersveld (1951), Vinokurov (1960), Dillery (1965) and Swanson and Bartonek (1970) have pointed out that different foods break down and disappear differentially from gizzards (the major region of the stomach), the rate of disappearance of each depending largely on the extent of sclerotization or portion of hard parts. This view is upheld by the marked differences between the relative proportions of foods stored in the crops of waterfowl and those found partly digested in accompanying gizzards (Bartonek and Hickey, 1969; Dirschl, 1969). Quantitative dietary studies of omnivorous birds based solely on identification of food remains in their gizzards obviously overestimate items difficult to digest. In this study of starling feeding ecology, the times of real and relative rates of breakdown and disappearance of common foods from the gizzard were determined to quantify the apparent diet patterns established from numeric analyses of gizzard contents. Estimates assume an approximate constant rate of intake of each species. This appears valid as the wide range of food species recovered from individual gizzard and nestling collar samples (see Ch. 6.3.IV & V respectively) point to isolated rather than sequential capture of most foods taken. Colonial forms like sarcophagid fly larvae are probably the exception, but these and other foods are randomized by sample lumping.

2. METHODS

In February 1971, 51 newly captured starlings were held in an indoor cage for three days to acclimate to laboratory

Table 26. THE RATE OF DISAPPEARANCE OF FOOD ITEMS FROM THE GIZZARD OF STARLINGS

Food Species		Digestion period (min)									
		15		30		60		120		180	
		N^+	$\%P^+$	N	%P	N	%P	N	%P	N	%P
Costelytra zealandica	A^o	15	100.0	17	70.6	13	30.8	11*	0.0	4	0.0
" "	L^o	20	100.0	24	87.5	16	62.5	18	33.3	4	0.0
Tenebrio sp.++	A	13	100.0	15	100.0	12	91.7	6*	0.0	2	0.0
" "	L	20	100.0	24	70.8	15	26.7	12	8.3	4	0.0
Apion ulicis	A	24	62.5	33	45.5	26	26.9	20	0.0	8	0.0
Muscidae-gen.undet.	A	13	76.9	19	47.5	12	16.7	8	0.0	4*	0.0
" "	L	18	100.0	24	62.5	16	0.0	12	0.0	4	0.0
Lycosidae-gen.undet.	A	8	62.5	14	35.7	12	8.3	7	0.0	2	0.0
Coleophora spp.	L	20	100.0	22	77.7	6	68.8	13	66.6	5	0.0
Lumbricidae-gen.undet.	-	6	16.6	18	0.0	7	0.0	5	0.0	3	0.0
Triticum sativum		5	100.0	14	100.0	4	100.0	4	100.0	2*	0.0
No. of starlings in sample		10	-	12	-	8	-	9	-	2	-

Note: N^+ - No. of items ingested $\%P^+$ - Percent of quantifiable remains after period of digestion

++Tenebrio sp. - Considered representative of large Coleoptera taken in the field

* - Non-quantifiable traces only A^o, L^o - adult and larval stages respectively

conditions. Adequate water and a food supply of mince-meat and laboratory-reared arthropods were provided; only seven birds lost weight during this period.

Following the acclimation period each bird was subjected to a "feeding trial" which consisted of solitary confinement overnight, the acceptance next morning of a mixed standardised meal, and death after a period ranging from 15 to 180 min. Ten birds were uncooperative and were released. Those remaining (41) were supplied with a distinctive food (mince-meat) until 15 min before the trial meal and this was replaced after the meal had been ingested or rejected.

Each meal consisted of two live individuals of adult and larval grass grubs, adult and larval flies, adult and larval Tenebrio beetles, earthworms, spiders, grains of wheat, and four weevils and Coleophora larvae (Lepidoptera). During the trials, feeding animals were closely watched through one-way glass and uneaten items noted.

After death the experimental birds were treated identically to those collected for food studies in the field (see Ch. 6.2.III.). Subsequently, the nature and frequency of quantifiable remnants of each food present in the gizzard were compared with that ingested, to determine correction factors. Further analysis followed that outlined by Mook and Marshall (1965), who considered that for a constant rate of ingestion of invertebrate foods by the olive-backed thrush Hylocichla ustulata, the ratio of identifiable foods remaining in the gizzard to the total number eaten during a two hour period before death, was a function of the rate of disappearance during that period i.e. the percentage retained after any time interval equalled Area B / Area A + B (see Fig. 19).

3. RESULTS

Starlings immediately devoured whole most constituents of the meals presented. Food species differed in their breakdown rates (Plate 4) and hence the rates at which quantifiable portions disappeared from bird gizzards (Table 26) i.e. such portions as head capsules, both mandibles, elytra or other elements which permitted a real assessment of the animals eaten.

Earthworms disappeared most rapidly, only setae being

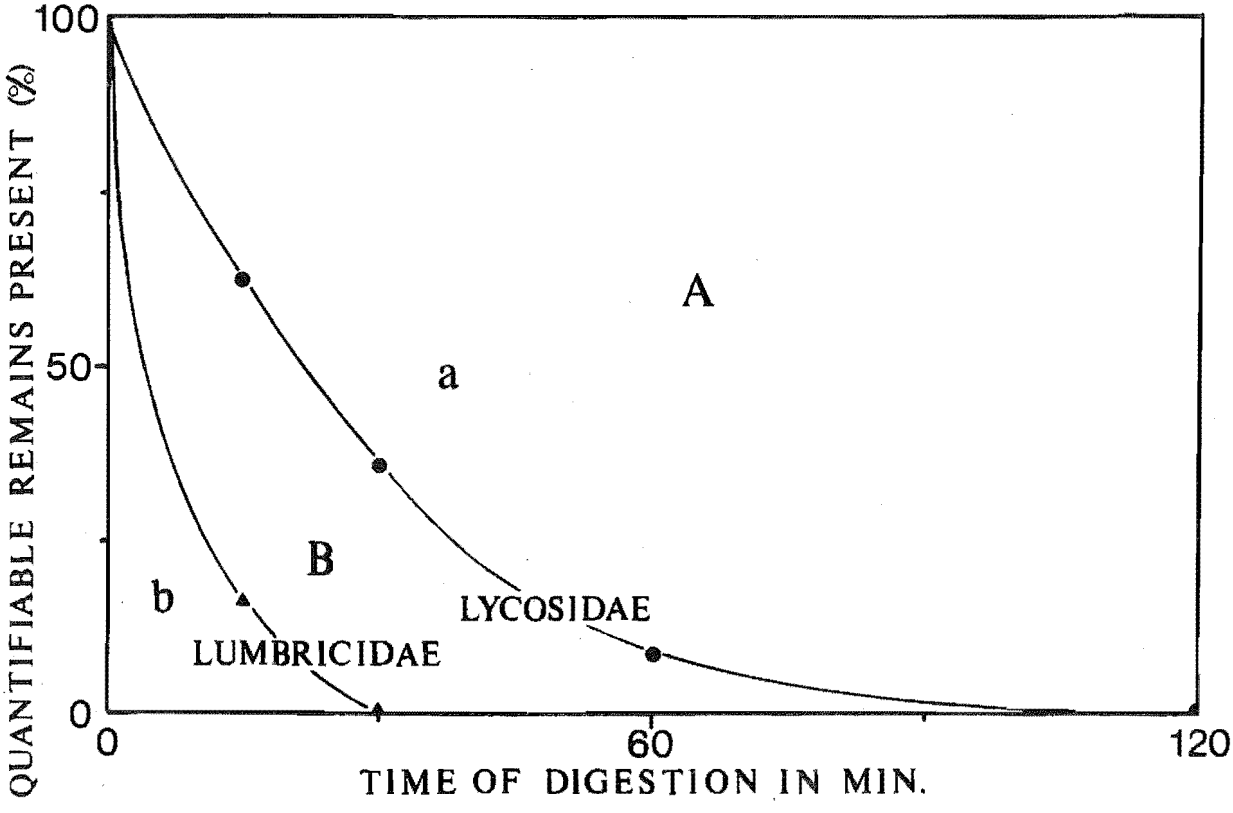
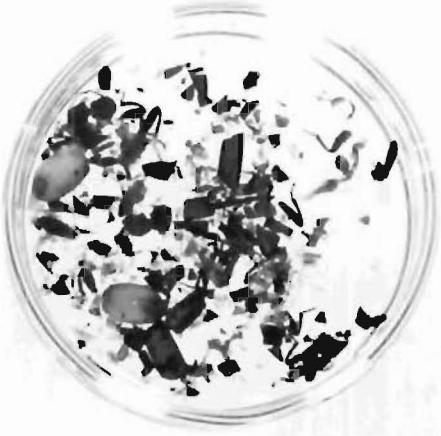

100
50
0
0
60
120
QUANTIFIABLE REMAINS PRESENT (%)
TIME OF DIGESTION IN MIN.
A
a
B
b
LYCOSIDAE
LUMBRICIDAE

Fig. 19

Rates of disappearance of two major foods from the gizzard of starlings. The percentage of each species retained after 120 min of feeding is equal to Area B / Area A + B.

a



b

c

d

e

Plate 4. THE FORM OF FOOD ITEMS AFTER DIFFERENT PERIODS OF DIGESTION IN THE GIZZARD OF STARLINGS (PHOTOGRAPH - J. BURNIP).

Digestion Period (Min).	Usual Form of Food
15 (a)	Earthworms and small species often lost. Larval forms, adult flies and arachnids squashed. Adult beetles slightly dismembered. Cereal and Coleophora spp. whole.
30 (b)	As above plus - earthworms and arachnids rarely present. Larval forms indicated only by head capsules, adult beetles by intact heads but fragmented bodies. Adult flies present as traces.
60 (c)	As above plus - adult and larval flies and adult weevils generally not present. Beetle larvae represented by free mandibles, adults by fragmented head capsules. Cereal and Coleophora spp. tattered.
120 (d)	As above plus - beetle adults and larvae in traces apart from mandibles. Cereal and Coleophora spp. fragmented.
180 (e)	Non-quantifiable traces of the harder forms only.

detected after 15 min. Small soft-bodied forms like spiders, fly adults and larvae, and weevils also disappeared quickly, only 36, 47, 62 and 45% respectively remaining after 30 min. One hour after ingestion, larger beetles and their larvae were often non-quantifiable i.e. 31, 63 and 27% of ingested adult and larval Costelytra and larval Tenebrio sp. present respectively, while after two hours only cereal and the cases of larval Coleophora spp. remained whole. No quantifiable remains were recorded 3 hr after ingestion. For similar foods in the meadowlark Sturnella neglecta (Bryant, 1914) and some corvids (Van Koersveld, 1951), the order of loss, but not the exact rates, approximated results for the starling.

Table 27. ESTIMATES OF COMMON FOODS QUANTIFIABLE AFTER TWO HOURS OF REGULAR FEEDING

Food Species		No. estimated to be present after 2 hr (%)	Correction factor *
Costelytra zealandica	A^+	40.4	2.5
" "	L^+	67.4	1.5
Tenebrio sp.	A	74.0	1.4
" "	L	72.4	1.4
Apion ulicis	A	29.8	3.4
Muscidae-gen.undet.	A	28.2	3.5
" "	L	30.0	3.3
Lycosidae-gen.undet.	A	22.4	4.5
Coleophora spp.	L	75.4	1.3
Lumbricidae-gen.undet.	A	4.5	22.2
Triticum sativum	-	100.0	1.0

Note * - for explanation of correction factor, see text.
A^+ and L^+ - adult and larval stages respectively.

The "expected" percentage of each food present two hours after ingestion and the correction factor derived from this varied considerably (Table 27) e.g. approximately 22% of all

lycosid spiders eaten over a 2 hr period before death will be quantitatively recognisable at the end of it i.e. the number ingested is 4.5 times the number subsequently found in the birds gizzard. For cereals, 100% of that ingested will still be recognisable after 2 hr, so the amount ingested is equal to the amount present.

4. DISCUSSION

A reliable method of assessing the foods taken is imperative in any dietary study. In the starling's gizzard, food species are lost differentially and the greater the time lapse between ingestion and death (and a subsequent fixation of the gizzard contents), the greater the bias towards harder foods present. Thus, for this bird species, and probably most others, the numbers of foods present in the gizzard at any time do not represent true proportions of the numbers ingested. However, the latter may be determined from the rate of loss shown by each species eaten. In the present study, correction factors have been calculated for common or representative food species, and extrapolation to identical or similar forms taken in the field enables the calculation of real rather than apparent numbers of foods taken.

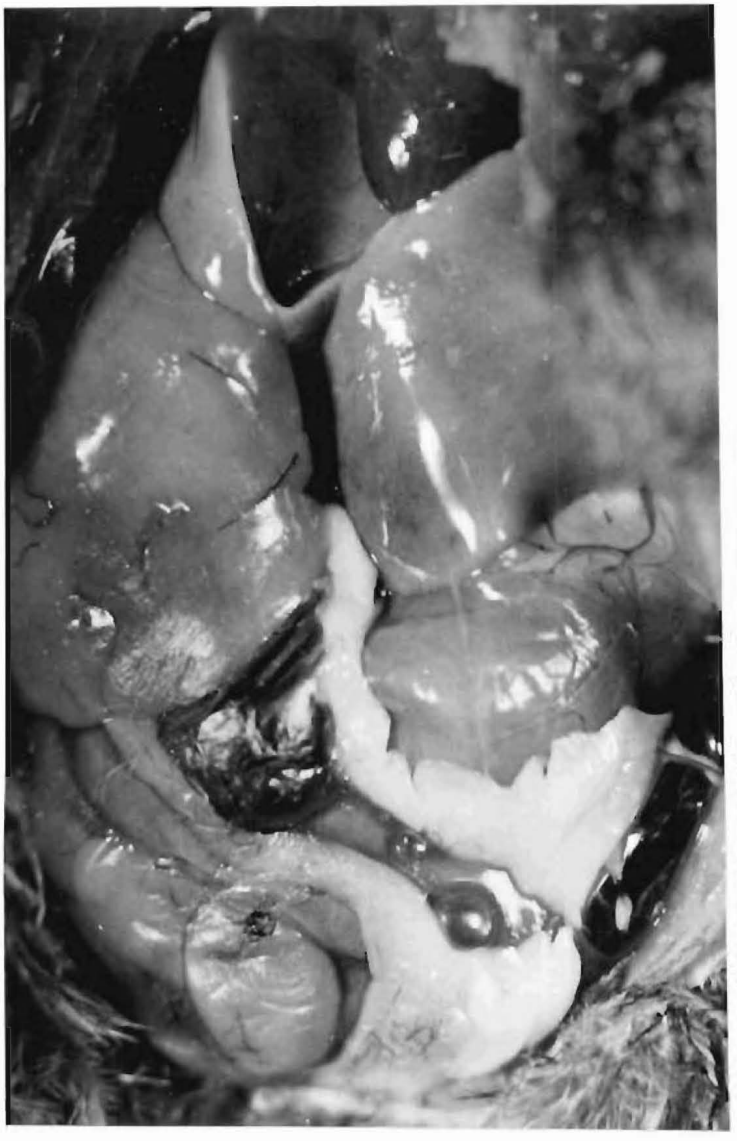


Plate 5

The visceral fat depot of starlings.

(Photograph - H.A. Best)

CHAPTER 8

CHANGES IN BODY WEIGHT

1. INTRODUCTION AND METHODS

The physiological well-being of an animal or population is largely dependent on the nature and amount of food it ingests, and is predictable from live weight changes following weight changes of its organs. This study analysed variations in the weight of live starlings, their liver, ether-extractable "fats" (fats, paraffins, waxes and alcohols), fat-free tissues and gizzard contents, and evaluated seasonal well-being of first year and adult males and females.

The collection of starlings has been described separately (see Ch. 6.2.III.). Approximately 400 carcasses were sexed, aged, weighed (= "live weight") to the nearest 0.1 g on a Mettler pan balance and then frozen for subsequent analysis. Each carcass was later thawed and the intact liver, gonads, gizzard contents and perivisceral fat depot removed and weighed separately on the same balance. The latter, a discrete depot underlying the viscera adjacent to the rectum, provided an estimate of total fat for all birds (Plate 5). The fat extractable by petroleum ether (B.P. 40 - 60° C) was determined for birds collected in March, June, September and December; these months being representative of the four seasons. Methods of extraction were adapted from Rogers and Odum (1964) and Bamford (1970). Each carcass, with plumage intact but minus the intestine, gizzard contents, liver, perivisceral fat depot and gonads, was cut into several pieces and finely minced in a laboratory "Waring" blender. The intestine minus obvious fat was discarded because of errors arising from the presence of digested food. The minced remains were dehydrated in an oven at 60° C to establish dry weights. Fat was extracted from each dried specimen by three successive boilings in petroleum ether in a constant-temperature water bath. Solvent from each boiling was subsequently filtered, and after the third filtration the samples again dehydrated and weighed to obtain the weight of dry fat-free tissues and, indirectly, ether-

Table 28. ANALYSES OF VARIANCE OF THE LIVE WEIGHTS OF STARLINGS WITH SEX AND AGE

A. SEX

First year birds

Season	Live weights (g) Male	Female	Degrees of freedom	Fs	Level of significance
Autumn	83.54	79.92	1,25	3.454	n.s.
Winter	85.37	80.22	1,14	2.509	n.s.
Spring	87.10	81.19	1,14	5.860	*
Summer	76.17	72.79	1,15	1.556	n.s.

Adult birds

Yearly aggregate	88.01	82.14	1,194	55.06	***

B. AGE

Males

	Adult	First year			
Autumn	84.94	83.54	1,36	0.235	n.s.
Winter	90.48	85.37	1,49	5.390	*
Spring	87.75	87.10	1,48	0.131	n.s.
Summer	87.40	76.17	1,22	47.300	***

Females

	Adult	First year			
Autumn	81.58	79.92	1,31	1.230	n.s.
Winter	83.54	80.22	1,35	1.272	n.s.
Spring	82.22	81.19	1,37	0.284	n.s.
Summer	81.07	72.79	1,24	9.944	**

extractable fat. As a check on the extraction methods, 10 carcasses were boiled a fourth time and, within the limits of the equipment used, no further weight lost. The total fat of birds other than those used in chemical extractions was predicted from regression equations developed by regressing the perivisceral fat on total fat; the equations for each season being:

March	Y	=	0.406 + 0.490 X
June	Y	=	0.665 + 0.173 X
September	Y	=	0.486 + 0.442 X
December	Y	=	0.384 + 0.638 X

The variation in the fat content of all starlings collected relative to body weight was examined indirectly by regressing live weights on fat-free body weights (= live weight - total fat) and comparing the regressions using analysis of covariance techniques (see Snedecor and Cochran, 1967). Finally, seasonal variation in the live weight of birds, their livers, total fat, fat-free tissues and gizzard contents were tested with a posteriori single classification analysis of variance techniques followed, where significance occurred ($p < 0.05$), by Gabriels' sum of squares simultaneous test procedure (SS-STP; Sokal and Rohlf, 1969, p.237). SS-STP analyses rank samples in decreasing magnitudes of their means, with means not covered by two lines and enclosed by the range of any one line (see text), significantly different from others. Variation with age and sex of the same carcass variates was tested subsequently using single classification analysis of variance (Sokal and Rohlf, op.cit., Ch.9).

2. RESULTS

I. Live weight

The live weights of starlings were greatest in winter and least in summer; a trend typical of birds (Baldwin and Kendeigh, 1938). Adult seasonal variation did not differ significantly from zero, presumably because of high intra-sample variation i.e. males decreased seasonally from 90.48 $\pm$ 0.896 to 84.94 $\pm$ 1.310 g and females from 83.54 $\pm$ 1.230 to 81.07 $\pm$ 1.309 g c.f. mid-winter maximums for

Table 29. ANALYSES OF VARIANCE OF FRESH LIVER WEIGHTS OF STARLINGS WITH SEX AND AGE.

A. SEX

First year birds

Season	Liver weights (g) Male	Female	Degrees of freedom	Fs	Level of significance
Autumn	3.05	2.55	1,17	4.503	*
Winter	2.87	3.48	1,14	1.586	n.s.
Spring	3.11	3.25	1,13	0.258	n.s.
Summer	2.98	3.27	1,14	1.201	n.s.

Adult birds

	Male	Female			
Autumn	2.89	2.72	1,21	0.866	n.s.
Winter	3.61	3.27	1,71	4.510	*
Spring	3.25	3.07	1,70	1.151	n.s.
Summer	3.21	2.84	1,27	4.289	*

B. AGE

Males

	Adult	First year			
Autumn	2.89	3.05	1,24	0.792	n.s.
Winter	3.61	3.87	1,51	1.205	n.s.
Spring	3.25	3.11	1,48	0.193	n.s.
Summer	3.21	2.98	1,23	1.286	n.s.

Females

	Adult	First year			
Autumn	2.72	2.55	1,14	0.597	n.s.
Winter	3.27	3.48	1,34	0.535	n.s.
Spring	3.07	3.25	1,35	1.159	n.s.
Summer	2.84	3.27	1,18	3.280	n.s.

adult male and female starlings in North America of 87.42 and 82.73 g respectively (Hicks, 1934). Live weights of first year Canterbury birds followed patterns set by adults (also shown by Dunnet, 1956), with summer weights significantly lower than spring and autumn weights in females and spring, autumn and winter weights in males i.e.

Mean live weight (g)

	Spring	Autumn	Winter	Summer
First year females	81.2	80.2	79.9	72.8
First year males	87.1	85.4	83.5	76.2

Male starlings were generally heavier than females of similar age (Table 28). Adults differed significantly in their aggregate means but first year birds differed only in spring as they approached adult weight. Adults on average were heavier than first years; significant differences occurring between females in summer, and between males in summer and winter. Starlings of both sexes are smallest in summer following fledging, but close to adult weight by the subsequent autumn.

II. Liver weights

Liver weights varied seasonally. Trends amongst sex and age groups were similar, with the livers of all birds significantly heavier in winter than in autumn. First year males also showed significant winter and summer differences i.e.

Intact Liver Weights (g)

	Winter	Spring	Summer	Autumn
Adult females	3.27	3.07	2.84	2.72
Adult males	3.61	3.25	3.21	2.89

	Winter	Summer	Spring	Autumn
First year females	3.48	3.27	3.25	2.55

	Winter	Spring	Autumn	Summer
First year males	3.87	3.11	3.05	2.98

Table 30. ANALYSES OF VARIANCE OF THE TOTAL FAT OF STARLINGS WITH SEX AND AGE

A. SEX

First year birds

Season	Total fat (g) Male	Female	Degrees of freedom	Fs	Level of significance
Autumn	3.64	3.65	1,20	0.002	n.s.
Winter	7.39	5.68	1,14	4.426	n.s.
Spring	4.42	3.99	1,14	1.124	n.s.
Summer	3.19	3.14	1,14	1.058	n.s.

Adult birds

Autumn	3.71	4.28	1,40	1.434	n.s.
Winter	7.51	7.24	1,69	0.156	n.s.
Spring	4.93	5.87	1,69	2.592	n.s.
Summer	3.49	4.05	1,31	2.706	n.s.

B. AGE

Males

	Adult	First year			
Autumn	3.71	3.64	1,35	0.057	n.s.
Winter	7.51	7.39	1,49	0.011	n.s.
Spring	4.93	4.42	1,48	0.471	n.s.
Summer	3.49	3.19	1,23	0.139	n.s.

Females

	Adult	First year			
Autumn	4.28	3.65	1,25	0.891	n.s.
Winter	7.24	5.68	1,34	3.742	n.s.
Spring	5.87	3.99	1,35	2.730	n.s.
Summer	4.05	3.14	1,22	2.456	n.s.

Adult males generally had heavier livers than adult females; differences being significant in winter and summer (Table 29). Patterns amongst first year birds were less regular although significant autumnal differences were recorded. Age differences were not established, but livers of first year starlings generally were as heavy or heavier than those of adults.

III. Total fat weights

Total fat varied seasonally. Trends were similar for each sex and age category, with average total fat maximal in winter and minimal in summer following the fledging or breeding of first year and adult birds respectively. Winter fat was commonly significantly greater than in any other season i.e.

Total Fat (g)

	Winter	Spring	Autumn	Summer
Adult females	7.24	5.87	4.34	4.17
Adult males	7.51	4.90	3.71	3.47
First year females	5.68	3.99	3.62	3.14
First year males	7.39	4.41	3.64	3.58

Total fat did not differ significantly with either age or sex (Table 30). However, first year females generally had less fat than adult females or like-aged males. Conversely, adult females frequently had more fat than adult males.

The relative fat content, determined indirectly, of birds of different ages varied seasonally (Fig. 20, A - D). Unfortunately, high sample variances of one or both age groups limited analyses of covariance comparisons. Even so, in autumn and winter (Fig. 20, A & B) it appeared that greater fat-free weights and hence total fat were attained by adult starlings compared with younger birds of the same body weight. Conversely, in spring and summer (Fig. 20, C & D) first year birds appeared to have higher fat-free and total fat weights than similar sized adults.

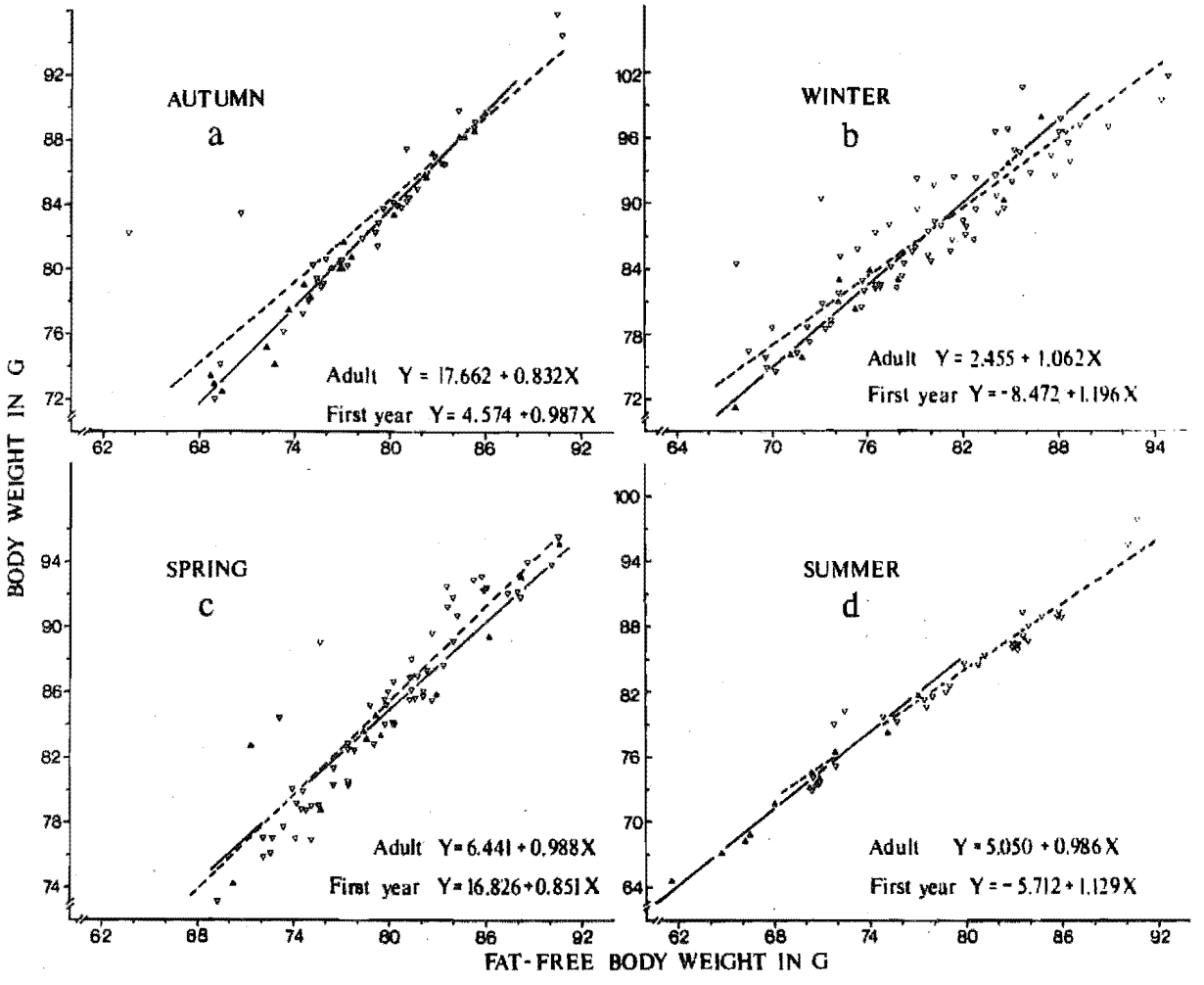

AUTUMN
a
Adult Y = 17.662 + 0.832X
First year Y = 4.574 + 0.987X
WINTER
b
Adult Y = 2.455 + 1.062X
First year Y = -8.472 + 1.196X
SPRING
c
Adult Y = 6.441 + 0.988X
First year Y = 16.826 + 0.851X
SUMMER
d
Adult Y = 5.050 + 0.986X
First year Y = -5.712 + 1.129X
BODY WEIGHT IN G
FAT-FREE BODY WEIGHT IN G

Fig. 20

Seasonal regression analyses of body (live) weight on fat-free body weights of adult (-- ▽ --) and first-year starlings (- △ -).

Table 31. ANALYSES OF VARIANCE OF THE FAT-FREE WEIGHTS OF STARLINGS WITH SEX AND AGE

A. SEX

First year birds

Season	Fat-free weights (g) Male	Female	Degrees of freedom	Fs	Level of significance
Autumn	80.53	75.17	1,20	7.166	*
Winter	78.00	74.66	1,14	1.482	n.s.
Spring	81.80	77.24	1,14	2.735	n.s.
Summer	72.61	68.45	1,14	3.209	n.s.

Adult birds

Yearly aggregate	82.42	76.12	1,188	81.026	***

B. AGE

Males

	Adult	First year			
Autumn	80.87	80.53	1,32	0.039	n.s.
Winter	82.99	78.00	1,49	6.851	*
Spring	82.99	81.80	1,48	0.345	n.s.
Summer	83.77	72.61	1,23	56.615	***

Females

	Adult	First year			
Autumn	76.24	75.17	1,25	0.207	n.s.
Winter	75.44	74.66	1,34	0.153	n.s.
Spring	77.42	77.24	1,35	0,340	n.s.
Summer	77.13	68.45	1,22	10.848	**

IV. Fat-free weights

Fat-free weights of adult starlings were greatest in summer and spring and least in autumn and winter for males and females respectively, but seasonal differences were not significant e.g. males varied from 83.77 ± 0.980 to 80.87 ± 1.249 g and females from 77.42 ± 0.934 to 75.44 ± 0.888 g. Conversely, first year birds showed significant seasonal variation and were lighter in summer than in spring (females) or autumn and spring (males) i.e.

Mean Fat-free Weights (g)

	Spring	Autumn	Winter	Summer
First year females	77.2	75.2	74.7	68.5
First year males	81.8	80.5	78.0	72.6

The fat-free weights of male starlings were generally greater than those of females of similar age, with adults differing significantly in their annual aggregate means and first year birds in autumn (Table 31). Adult fat-free weights were greater than those of first year birds throughout the year, with females differing significantly in summer and males in summer and winter. Variations in fat-free tissues result from the small summer size of first year birds imposed on an overall dimorphic pattern.

3. DISCUSSION

The live weights of adult starlings vary seasonally depending on the regular deposition or mobilization of fat and other analogous stored products (Fig. 21). Increases in total fat were matched by increases in liver weight; the latter due to changes in stored glycogen (carbohydrate), fat, protein and water (Ljunggren, 1968). The liver serves as a food-storage organ and increases in its weight, especially when coincident with increases in total fat, must be indicative of periods when the bird is consuming food in excess of its immediate requirements.

Seasonal decreases in live weights, food storage organs and depots, varied in timing and magnitude with sex. Males,

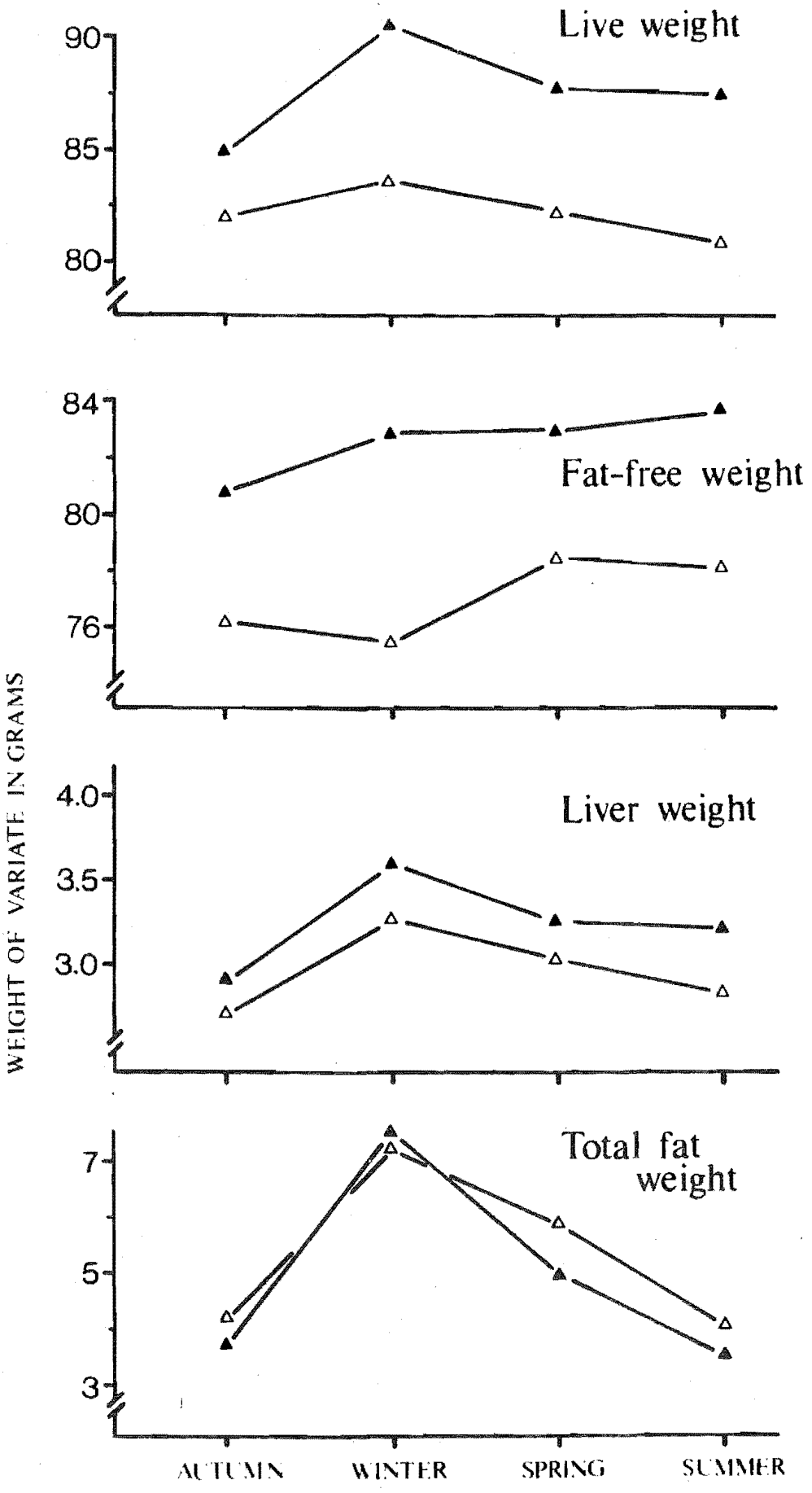

Live weight
90
85
80
Fat-free weight
84
80
76
Liver weight
4.0
3.5
3.0
Total fat weight
7
5
3
WEIGHT OF VARIATE IN GRAMS
AUTUMN
WINTER
SPRING
SUMMER

Fig. 21

Seasonal variation in live weight, fat-free tissues, liver and total fat weight of adult starlings. Males (▲) and females (△) show similar trends; most components being heaviest in winter and lightest in autumn and summer.

though heavier than females, lost 5.29% of their mid-winter live weight by the start of laying. On the other hand, females lost 3.51% of their winter weight by the end of the nestling period; a rate of loss less than half that of males. Such disparities appear to result from the division of labour of the two sexes prior to and during breeding. Males select and defend nest sites before laying commences (see Ch. 5.3.V), but females spend longer periods at the nest following laying and convert considerable liver reserves into egg yolk (Bellairs, 1964); both activities probably result in partial inanition (want of nourishment) and, as suggested by Baldwin and Kendeigh (1938), partly determine the observed losses in weight of liver and fat depots.

Relative fat content varied with the age of starlings. Although heavy birds generally had large fat reserves and vice versa, medium-sized birds were not so predictable, due largely to age differences. In comparison with older birds, those in juvenile plumage in summer had relatively large fat reserves, due to intensive feeding by parents before and after leaving the nest. Likewise, first year birds in spring had large reserves, as generally they did not breed. Conversely, adults in spring and summer had relatively low fat reserves apparently because of the intensive activities of breeding. In autumn and winter this pattern changed. Adults had relatively greater fat reserves than younger birds, which suggests that when the activities of all birds were similar, adults fed more successfully (also shown for wood pigeons, see Lack, 1966, p185).

The fat-free tissues of adult Canterbury birds did not vary seasonally, which agrees with the findings of Connell, Odum and Kale (1960) for a range of passerine species. Conversely, much of the seasonal variations in live weights of migrant and non-migrant passerines has been reported to result from variations in fat-free tissues metabolized following the seasonal depletion of fat reserves (see Newton, 1969; Child, 1969, Fry, Ash and Ferguson-Lees, 1970, Barnett, 1970).

Seasonal variations in the stored 'food' reserves of Canterbury birds, point to seasonal differences in feeding rates (as shown for starlings in North America, see Hart, 1962) or caloric requirements. It is not necessarily indicative of variations in food availability; some mammals lay down fat during periods of comparative food shortage (Flux, 1971).

Variations in the wet weight of gizzard contents of West Melton birds analysed by analysis of variance, were independent of season, sex and age c.f. seasonal variation recorded by Havlin and Folk (1965). Contrary results have been obtained for starlings and other passerines in North America (Stevenson, 1933), where first year birds on average contained more food in their gizzard than did adults. Although the gizzard and proventriculus of the starling serve in part as storage organs, variations in breakdown rates and hygroscopic qualities of seasonally taken Canterbury foods, and the frequency and strength of gizzard contractions (Sturkie, 1954), apparently obscure any seasonal differences in rates of ingestion. However, as the starling's diet is characterized by distinct seasonal prey components which vary markedly in their caloric content (see Ch. 6.3.IV), it is possible that the caloric intake, if not the weight of food taken, may vary seasonally. This would not necessarily need to be true during breeding, when increased activity and a subsequent moult (see Kessel, 1957) preclude the deposition of reserve foods. Ljunggren (1968) similarly considered that live and fat weights of the wood pigeon in Sweden were determined by the quality not quantity of their food, with large quantities of food low in caloric value being taken during "lean" periods of the year.

Table 32. A REANALYSIS OF THE ENERGETICS OF THE DOMINANT FOODS OF FREE-FLYING STARLINGS (From Table 20).

Food form		No. of items taken from gizzards	Total energy of digestible tissue in gizzard (Cal)	Correction factor for each food group (see Table 27)	Relative total energies of tissues eaten (Cal)
Hemiptera	A.	5328	27.55	3.5	96.43
Lepidoptera	L.	4720	542.79	1.5	814.19
Diptera	A.	168	4.75	3.5	16.63
Curculionidae / Tenebrionidae	A.	11046	95.42	3.4	324.43
Carabidae / Scarabaeidae / Elateridae	A.	1379	105.71	2.5	264.28
Scarabaeidae / Elateridae	L.	2383	237.42	1.5	356.13
Lycosidae		1008	46.37	4.5	208.67
Lumbricidae		141	30.46	22.2	676.21
Cereal		-	225.00	1.0	225.00

Note: - Each food form includes only those species listed in Table 20.
Correction factors for adult Hemiptera and larval Lepidoptera were taken as the values calculated for adult Diptera and larval Coleoptera respectively.

CHAPTER 9

GENERAL DISCUSSION

1. A REASSESSMENT OF THE FOODS OF FREE-FLYING STARLINGS

The foods ingested by starlings breakdown differentially. Numerical analyses of gizzard contents bias dietary patterns towards harder foods present, but realistic patterns may be obtained through the use of factors which correct for differential digestion rates (see Table 27). Caloric estimates of each dominant food group obtained from numeric counts then assume new proportions relative to one another (Table 32), with soft-bodied foods forming a bigger proportion of the annual diet. With revaluation, Lepidoptera larvae remain paramount. Lumbricid earthworms supercede all remaining forms, lycosid spiders, Hemiptera and Curculionidae increase markedly but cereal grain decreases in importance. Overall, the caloric value of dominant foods consisted of 82.9% animal and 17.1% plant tissues prior to reassessment, but subsequently of 92.5% animal and 7.5% plant tissues.

2. STARLINGS AS PREDATORS OF GRASS GRUBS

Many birds have been credited with the ability to control populations of insect pests. Accurate estimates of the prey numbers ingested and the levels of control attained have been limited to a few recent studies, however, notably of forest dwelling birds e.g. Pardalotes, especially Pardalotus ornatus feeding on psyllids in South Australia (Clark, 1964); a range of Canadian birds on the larch sawfly - Pristiphora erichsonii (Buckner and Turnock, 1965); woodpeckers - Picoides spp. and Dendrocopos spp. on the Engelmann spruce beetle in the U.S.A. (Knight, 1958; Baldwin, 1968); currawongs - Strepera graculina on phasmatid species in Eastern Australia (Readshaw, 1968). In these studies, control by avian predators occurred only in areas of low prey density, thus supporting Kales (1968) statement viz. "No evidence exists that any avian species can effectively control a species of insect upon which it feeds when that pest is at or near peak

abundance".

Starlings have been thought to control agricultural insect pests. Excluding anecdotal reports, in Europe they have controlled local populations of the colorado beetle Leptinotarsa decemlineata - a chrysomelid harmful to potatoes (Zacki, 1960; Gromadski, 1969), and the cockchafer M. melolontha - a common scarabaeid beetle harmful to pasture (Pfabe and Szypula-Gador, 1964). In New Zealand, interest has been focused on starling - grass grub relationships; the latter another scarabaeid similar in habit to M. melolontha. Hence, although Caithness (1968) stated that contrary to common belief "starlings are not capable of any significant biological control of scarabid larvae", Anonymous (1970) detailed results from Winchmore Experimental Station, Canterbury, where starlings alone reduced larval grass grub populations in irrigated pasture from 100 to 60 / ft^2 (929 cm^2) and associated with sheep from 100 to 9 / ft^2. However, results at Winchmore were obtained under unusually favourable conditions; a large roost was located near the farmlet where intelligent farm management, high grass grub numbers and numerous nest boxes attracted large numbers of birds.

The life cycle of the New Zealand grass grub has been established (see Kelsey, 1951). In brief, adults first emerge between November and February and within two weeks females lay eggs in surface soils. These hatch 16 - 21 days later and the larvae descend to depths greater than 5 cm to feed on grass rootlets. Four to five and 9 - 16 weeks later the larvae moult and during the resultant instars (second and third), live in the top 5 cm of soil. Larvae pupate from July to September over a period of 4 - 6 weeks at depths of 10 - 25 cm and later emerge nocturnally as adults for a few weeks of reproduction and feeding. The beetles burrow back into the soil each day until senile, when they die on the surface (East, 1972, p327).

Grass grubs are thus available to starlings as adults in late spring and early summer, and as second and third instar larvae from late summer to mid-winter. At other times the various life stages occur at depths of greater than 5 cm and normally are out of reach.

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Independent starlings at West Melton eat grass grub beetles between October and late December and from them obtain approximately 2.4% of their annual ingested energy. Beetles are a staple food of nestlings in late November to early December and provide 16% of their ingested energy. However, regardless of the number taken, predation probably has a neglible effect on grass grub populations. Of 80 female beetles taken from nestlings, only two contained eggs; the remainder were post-breeders and, along with males, were probably taken at or after death from the sward surface.

Grass grub larvae (third instar only) are ingested by independent starlings between late March and August and form approximately 16% of the birds annual caloric intake. Larvae are taken in greatest numbers in May (26 / bird collected on grass pasture) although birds which "follow the plough" in early spring often contain many more e.g. 40 - 60. In May, birds have approximately 10 hr feeding time (= daylight) during which the number of larvae ingested = 26 x 1.5 x 5 or 195 larvae / day, where 1.5 represents a correction factor for the number of larvae voided from the starlings gizzard within 2 hr of ingestion (see Table 27), and 5 the number of two hourly feeding periods available.

Starlings show a strong selection for larval foods, including grass grubs, and in autumn and winter feed commonly on grass pasture where grass grub larvae are available. Starlings rarely feed amongst lucerne, perhaps partly because once established, this plant is seldom attacked by grass grubs (Flay and Garrett, 1942). On grass pasture, third instar scarabaeid larvae may occur at densities of >100 / ft^2 (Kelsey, 1951; Anon, 1970). In comparison, starlings at West Melton occur at very low densities i.e. feeding densities of 0.55 birds / ha, and therefore appear insignificant as grass grub predators. However, starlings feed communally, often in large flocks, and through their selection of foods and feeding sites are able to prey on larvae more heavily than their numbers suggest. Predation rates can be further raised by artificial increases in local starling populations or the establishment of new ones (through the erection of nest boxes). However, unless efforts to increase starling numbers are accompanied by farm management orientated towards the

manipulation of the birds as biological control agents (e.g. Anon, 1970; East and Pottinger, In Press), little farmer-benefit will accrue.

3. FACTORS LIMITING STARLING NUMBERS IN CANTERBURY

Animal populations are widely believed to be controlled primarily through density-dependent factors (see Nicholson, 1933; Kendeigh, 1961). This theorem has received support by Lack (1954, 1966), who believes that mortality controlled largely by food availability is most important, with disease, parasites and predators of lesser consequence. Lack (1954, Ch.13) postulated that food shortage is often indicated indirectly by the movements of birds to areas of abundant food, by their frequent fighting over food, and by the ruling out of other mortality factors. However, food shortages are not the only density-dependent population control. Amongst others, many hole-nesting birds are apparently limited by a lack of suitable nest sites (for references, see Ch. 5.4.I).

In Canterbury, there is no direct evidence of acute food shortage and the resultant starvation of starlings. Dead birds were rarely recovered and starving starlings never. However, analyses of body fat suggest that in autumn and winter young birds may not find adequate suitable foods. At such times all starlings feed on less favoured and probably less nutritious foods e.g. cereal grain. Invertebrates are less common than in warmer periods, and during frosty periods only sward dwelling forms are available.

Starlings do not show marked seasonal variations in the incidence of fighting over food. They select feeding sites and food throughout the year, even when favoured foods are comparatively ubiquitous. Foraging ranges during breeding and non-breeding periods are generally smaller than those recorded in foreign studies, which suggests that local birds are less limited by food.

The losses of starlings through disease were not evident but, as in most bird species (Lack, 1954, Ch.15), probably were few. Levels of ecto and endo-parasitisation seemed unusually low. Helminths parasitising the alimentary canal were recorded in small numbers from 3.3% of 60 starlings collected at West Melton c.f. 100% infestation by helminths of

starlings collected concurrently at Harewood (see Johnson, 1969) and 78% infestation or more of starlings, depending on season, in Britain (Wynne Owen and Pemberton, 1962). External parasites occurred commonly but were rarely numerous enough to obviously be troubling the host. High infestations of lice (Mallophaga) were observed on only two independent birds and similar concentrations of mites (Acari) on the nestlings of one brood. Heavy infestations of mites on starling broods at Havelock North, New Zealand, are preponderant and make the handling of nestlings difficult (A. Moeed, scientist, pers. comm.), while in Arizona, U.S.A., similar infestations by the Red fowl mite (Dermanyssus gallinae) reduces starling breeding success (Royall, 1966).

West Melton starlings are commonly preyed on by one predator, the stoat, which often takes incubating or brooding birds. Females are particularly vulnerable as they spend more time in the nest than do males and unbalanced sex ratios amongst adults result. Stoats also eat nestlings, taking them when they are most vociferous e.g. minimally 5.6% of first broods. Predation of all starlings during the non-breeding period appears neglible.

Starlings appear to be limited by the availability of nest sites. Suitable artificial sites are rapidly colonized, even when erected during site selection 4 - 6 weeks prior to laying, and competition for them is intense. Birds return to particular nesting areas, and often to particular nest sites each year, and those which accept artificial sites are probably largely those formerly without a nest. Natural sites are markedly clumped, occurring primarily in farm buildings and rarely in other sites. The size of present populations in Canterbury and elsewhere is probably lower than in the past, when large flocks occurred in most lowland areas of New Zealand (Kirk, 1895; Bathgate, 1897; Thompson, 1922) and apparently are controlled primarily by changes in farm management, with an associated reduction in hedgerows and an increase in the use of ferro-concrete materials for fencing and farm buildings; suitable nesting cavities gradually being eliminated. Control through predation and food appear to be of lesser importance, and from disease and parasites little or none.

CHAPTER 10

SUMMARY

1. This work evaluates the activities of starlings in relation to man's interest in a rural ecosystem in Mid-Canterbury, New Zealand. It also describes the manipulation of local starling populations in regions of agriculturally harmful prey species.

2. Starlings were sexed from the sexually dimorphic iris and mandibular rami colours which, when used together, were completely reliable for males and almost so (99%) for females. Birds in adult plumage were aged from measurements of hackle feather iridescence and separated into first year and older birds; some could not be aged with certainty.

3. Counts of West Melton birds were greatest when made at winter roosts (1150). Fewer birds were recorded at feeding sites (618 $\pm$ 63) and half as few again at natural breeding sites.

4. Adult sex ratios were weighted towards males but were approximately 1:1 amongst nestlings and first year birds. The difference probably resulted from a greater mortality of females during breeding, especially of one year old birds.

5. Annual mortality was between 50 and 53% for adult females and approximately 12% for all first year birds; these figures are similar to those obtained in studies overseas.

6. The erection of suitable nest sites, particularly in hedgerows, led to local increases of starlings, which were enhanced in successive years by the tendency of adults to return to the same colony and often the same site each year. Consequently, intraspecific competition for artificial sites increased annually as local populations grew. Interspecific competition with house sparrows for nesting cavities also occurred commonly, especially amongst later breeding birds.

7. Starlings generally bred first when aged two, although a few precccious females did so at one. Males were physiologically incapable of breeding at one, although young birds often involved themselves in nest building and carolling activities.

8. Eggs were laid between mid-October and mid-December. Patterns were influenced by air temperatures, breeding age, and the time of fledging or loss of first and successive broods. Precise laying dates were determined by air temperatures, with cold periods during laying causing short laying cessations. Clutches on average ranged from 3.9 to 4.4 eggs and generally were smaller than those recorded in other countries.

9. Breeding success was greatest in first clutches and broods, and was maximal for the modal clutch sizes viz. 3, 4 and 5. Replacement and second clutches had little success and contributed only slightly to the overall productivity of the population.

10. Starling feeding behaviour varied seasonally. Birds foraged communally, either in small (< 100) uncoordinated groups which occurred throughout the year, or in large (>100) coordinated flocks characteristic of the non-breeding period. Foraging ranges were maximally 500 m from nests during breeding but up to 4 km from communal roosts at other times.

11. Starlings exhibited seasonal preferences for feeding sites and food. Birds periodically selected well-grazed pasture, cereal stubble, turnips and fields being tilled. Preferences were affected by stock, which were used by starlings as "beaters" and as observation posts. Birds apparently preferred larval to adult insects throughout the year, but especially so during the nestling period.

12. The diet of independent birds consisted predominantly of animal foods (approximately 90% by volume and caloric content), with the remainder largely cereal grain. Calorically, larval Lepidoptera, lumbricids and adult and larval Coleoptera were the staple foods, with arachnids and cereal grain important minor constituents. Hemiptera and Diptera were taken in large numbers but were of little caloric consequence.

13. The diet of nestlings was similar to that of older birds. Larval Lepidoptera, larval Coleoptera and Lumbricidae were staple foods, with Hemiptera and Diptera minor dietary elements.

14. Foods in the gizzards of starlings were digested and voided differentially and dietary patterns established from the contents of that organ were biased towards harder

foods present. Correction factors were calculated for staple foods and permitted more realistic dietary quantifications.

15. Starling live weights varied seasonally with the deposition or mobilization of fat and other stored products. Patterns were dimorphic, and in adults probably resulted from divisions of labour of the sexes prior to and during breeding. In spring and summer, non-breeding first-year birds carried relatively more fat than adults. However, adults appeared to feed more successfully than younger birds and when the activities of both age groups were similar (autumn and winter), adults had relatively more fat.

16. Starlings prey on two life stages of the grass grub, often taking large numbers of third instar larvae and adults. Significant reductions of this invertebrate are, however, probably only attained under the following specific conditions, practical only on a very local scale i.e. high populations of grass grubs, large resident populations of starlings, irrigated soils, and heavy stocking of infected pasture.

17. Starling numbers appear to be controlled largely through the availability of suitable nest sites. Young birds may have difficulty in finding sufficient suitable foods in winter, but direct evidence of mortality from shortages of food was lacking. Limited predation of adults and nestlings occurred during breeding seasons.

18. Overall, starlings at West Melton are probably beneficial. They take some cereal in winter from stock feedlots, but counterbalance this by preying on a wide range of insect species harmful to agriculture.

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APPENDIX I

THE GENERIC AND SPECIFIC NAMES OF ANIMALS AND PLANTS COMMONLY FOUND IN THE STUDY AREA

PLANTS

Cash Crops	wheat	*Triticum sativum*	barley	*Horodeum vulgare*
	oats	*Avena sativa*	potatoes	*Solanum tuberosum*
Fodder crops	turnips	*Brassica rapa*	rape	*Brassica napus*
	choumoellier	*B. aleracea*		
Exotic trees	pine	*Pinus radiata*	macrocarpa	*Cupressus macrocarpa*
	-	*Eucalyptus* spp.		
Others	gorse	*Ulex europaeus*	lucerne	*Medicago sativa*
	silver tussock	*Poa caespitosa*	fescue tussock	*Festuca novae-zealandiae*

ANIMALS

Farm stock	sheep	*Ovis aries*	cattle	*Bos taurus*
Feral mammals	cats	*Felis domesticus*	stoats	*Putorius erminea*
	hedgehogs	*Erinaceus europaeus*	hares	*Lepus europaeus*
	rabbits	*Oryctolagus cuniculus*		
Birds	rooks	*Corvus frugilegus*		
	white-backed magpies	*Gymnorhina hypoleuca*		
	gulls	*Larus dominicanus*, *L. bulleri*		
	house sparrows	*Passer domesticus*		
	rock pigeons	*Columba livia*		